SYSTEMATICS OF PROSOBRANCH GASTROPODS[1]

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ABSTRACT

The authors trace 5 main evolutionary lines within the class Gastropoda, and hence distinguish 5 principal taxonomic subdivisions, differing in the main characters of their structure. Three of these are, as a rule, united into the subclass Prosobranchia. However, the originality of morphological structure and direction of evolution in each of these 3 subdivisions are considered equivalent to those of the 2 other gastropod subclasses, the Opisthobranchia and Pulmonata. Three independent subclasses are therefore recognized among the prosobranch gastropods: Cyclobranchia, Scutibranchia and Pectinibranchia.

The Cyclobranchia (i.e. the former Docoglossa and some of the Paleozoic groups) present a particular line of evolution, demonstrable by their primitive, primarily symmetrical shell devoid of any incision or sulcus, by the archaic type of radular structure and movement, not shared by other Gastropoda, as well as by the structure of the reproductive system, stomach and nervous system, which are similar to those in Scutibranchia. Moreover, the asymmetry of the mantle complex, which the representatives of this group developed independently, the radula specialization, the development of the arterial bulbus and presence of the mantle nerve cords support the opinion that this group had a distinct type of evolution. From these considerations Cyclobranchia are set apart in a special subclass, embracing the orders Helcionellida, Archinacellida (formerly classified among the Monoplacophora) and Docoglossa. The evolutionary process was expressed morphologically within this group by the decrease in shell dimensions and sculpture, by the oligomerization of the radula, and by a reduction of the specialized breathing organs within the course of their development.

The rest of the Gastropoda originated from an ancient group of mollusks, evolving from primitive Cyclobranchia in the Cambrian period; these mollusks had a symmetrical mantle complex and a medially disposed fissure (selenizone) or sulciform projection.

The maintenance of symmetry of the mantle complex in the course of evolution, the parallel development of the fissure, the well developed epipodium and the absence of marked ganglia in the central nervous system, together with a marked development of symmetrical branchial ganglia permit unification of the orders Dicranobranchia, Fissobranchia and Macluritida into a separate subclass Scutibranchia. The evolution within Scutibranchia exhibits a tendency towards size reduction and decrease in degree of shell coiling, towards the separation and displacement of the selenizone from the peristome, a diminished importance of spiral sculpture as compared to axial sculpture, and the increase in size of the right kidney, due to its recently stabilized double function, that of excretion and of reproduction.

The subclass Pectinibranchia, including Monotocardia (Mesogastropoda and Neogastropoda) as well as Trochacea and Neritacea from Diotocardia (= Archeogastropoda) of former classifications, is phylogenetically the youngest and the most morphologically diverse; it has originated within Scutibranchia (most likely from Macluritida or their common ancestors).

Within Pectinibranchia 18 orders can be distinguished that share a common plan of structure and follow the general evolutionary trend of the whole subclass, but yet have a special line of evolution and a particular structure of shell, foot, digestive system, gill, central nervous system, reproductive system and ecology. From these 18 orders, the first to diverge were 2 groups, one now united in the superorder Pyramidellimorpha and the other comprising the superorder Turbinimorpha together with phylogenetically connected orders here combined in the new superorders Neritimorpha, Paludinimorpha, Littorinimorpha and Cerithiimorpha.

The evolution of the Pectinibranchia, which often manifests itself similarly in different superorders and orders, is expressed morphologically by the: decrease of (particularly spiral) sculpture; formation of a siphonal process in absence of the epipodium; reduction of jaw; oligomerization of radula, accomplished differently in different groups; increase of mantle complex asymmetry; formation of a pectinate ctenidium and osphradium; transformation of right kidney into renal gonoduct; and concentration and integration of the central nervous system. Evolution within different subdivisions of the Pectinibranchia went a parallel way, from ancestral microphagy, sestonophagy and phytophagy toward detritophagy, saprophagy and predation, and, within the specialized forms, toward parasitism. In the mode of reproduction it went from external to internal fertilization, to direct development and ovoviviparity.

Some evolutionary parallelism is perceived in the development of the subclasses under consideration. It is morphologically expressed in the tendency towards increased asymmetry of structure, oligomerization of the radular apparatus, a greater complexity of the reproductive system and a more pronounced concentration of the nervous system. In ecology and distribution, the evolutionary parallelism within the subclass manifests itself in the change of habitats (from life in shallow waters and on hard substrates to life at greater depths, on mixed and soft substrates, within epifauna and, later, infauna), in the adaptation to fresh water and terrestrial life, in the expansion of distribution from tropical and subtropical latitudes toward temperate and cold regions.

The phylogenetically most advanced groups have the largest numbers of living species within all subclasses and orders.

The evolutionary process within the Gastropoda under consideration was uneven and intermittent. The most intensive stages in the process of formation occurred simultaneously within different groups in the Cambrian-Ordovician, Permian-Triassic and Cretaceous-Paleogene periods.

INTRODUCTION AND DISCUSSION

The erection and varying composition of numerous classifications of Gastropoda (Pelseneer, 1906; Thiele, 1925-26, 1929, 1931; Wenz, 1938-1944; Korobkov, 1955; Pchelintsev et al., 1960; Taylor & Sohl, 1962; Pchelintsev, 1963) shows that scientists have made many attempts to explain and to express taxonomically the peculiarities of structural types and the diversity of evolutionary trends in this large and complex group of mollusks.

Even the subdivision of Gastropoda into subclasses, which at first sight seems stable and fully established, has lately been criticized and revised. The independence of the subclasses Opisthobranchia and Pulmonata has been recently discussed in detail (Boettger, 1955; Morton, 1963, and others). As to the subclass Prosobranchia, which has been less frequently discussed from that point of view, it was long ago pointed out that it could be characterized by not 1 but by at least 2 structural plans.

This lack of uniformity in opinion results from the fact that the complex of morphological characters which is taken as a criterion for the division of the Gastropoda into subclasses comprises mostly peculiarities in their level of organization. Within the period of gastropod evolution there more than once originated groups in different phylogenetic branches that were convergent as to type and complexity of organization, so that similarity of structure is not an indispensable condition for phylogenetic relationship.

To reveal the phylogenetic relationships and compose a natural system one should investigate whether certain peculiarities of structure are characteristic of forms belonging to the same phylogenetic line, or if different lines may hold them equally, having inherited the said peculiarities from their common ancestors; besides, one should know whether the representatives of dissimilar groups have developed the same peculiarities by simple convergence.

Considering the main principle of characterization of the gastropod subclasses, we can observe the following inconsistency: the chiastoneury which seems characteristic of Streptoneura (= Prosobranchia) and serves as a criterion for setting them apart from the 2 other traditional subclasses (Opisthobranchia and Pulmonata which are sometimes united as the Euthyneura), can be observed, strictly speaking, among the representatives of each of these subclasses. The difference lies in the fact that the majority of the Prosobranchia retain this peculiarity and are streptoneural, while only few of them have reduced or completely lost it (e.g. *Cingulopsis*), whereas within the Euthyneura, only the lowest representatives still possess chiastoneury (Acteonidae, Chilinidae, etc.)   while the

majority of the representatives have completely lost it. Moreover, the lack of chiastoneury within each of these subclasses may result from 2 independent processes, namely 1) from the shortening of the connectives, due either to greater concentration of the nervous system or, on the contrary, to the weakening of it, and 2) from detorsion.

The anterior position of the mantle complex, peculiar to Gastropoda, is lost within different subclasses, or is reduced to different degrees and for different reasons. This process is partly connected with the loss of primary symmetry in the mantle complex.

Two tendencies are distinguished in the evolution of the radula. The first manifests itself in a decrease in the number of teeth, from a considerable number (in rhipidoglossate forms), to 7 (in taenioglossate forms), to 2 (in toxoglossate forms), and even to 1 (in rachiglossate forms[2]). The diminution in the number of teeth could have developed independently, which can be illustrated by the fact that Epitoniidae and Janthinidae possess a multidental radula, Triphoridae and Choristidae a radula with more than 7 teeth, and Mathildidae, Omalogyridae and certain other families a paucidentate radula. A similar tendency in Docoglossa (the multidentate radula in Patellidae and the paucidentate one in Tecturidae) has already been discussed in the literature. The process of oligomerization within the Prosobranchia could have been accomplished in 2 ways: most frequently oligomerization manifests itself in the reduction and loss of marginal teeth; less commonly in the fusion of teeth, which is obvious in Lepetidae and highly probable in some Architectonicidae, as well as in Mitridae, Fasciolariidae and some other families.

The second tendency of radula evolution reveals itself in the predominance of the working part of the tooth accompanied by a reduction of its base, while the campilodont[3] rhipidoglossate and taenioglossate radulae independently transform into the orthodont[3] form in Ptenoglossa and Stenoglossa. The radula of some Architectonicidae

(e.g. *Architectonica*) seems to be transitional; the tooth inflection is still noticeable.

It is a fact of some interest that among Opisthobranchia and Pulmonata, the lowest forms (Acteonidae, Auriculidae and Chilinidae) also possess a campilodont radula, and only some of the representatives of these subclasses later acquired an orthodont radula.

Therefore the docoglossan radula cannot be considered a result of the development of any known campilodont and orthodont radula and resembles only the monoplacophoran and loricate radulae; the radula of the Docoglossa should thus be regarded as keeping the ancestral gastropod features.

The type of movement of the docoglossan radula is distinct too and similar to that of the Loricata and, probably, of the Monoplacophora.

The main characteristics of all the gastropod subclasses could have been similarly discussed one by one, but the above-mentioned items will suffice to show that formal treatment of even those characteristics which seem obvious at first sight presents considerable difficulty and that they must be treated with caution. Having no intention to undertake a complete revision of the classification of gastropods, we shall here only examine the relations within the prosobranchs, considering that the solution of this problem may later facilitate the creation of an improved system for the other subclasses.

If we examine the structure and evolution of the prosobranch mantle complex, excepting only the Docoglossa, we can reach the following conclusion. As has been stated above, the strictly symmetrical mantle complex may be considered an ancestral character for the majority of the Gastropoda. The lowest Paleozoic bellerophontid must have possessed such a strictly symmetrical mantle complex. A characteristic peculiarity of this type of mantle complex was that the rectum opened between 2 ctenidia, which required a complex apparatus to supply the ctenidia with clean water and to remove the water contaminated with faeces from the

[2]In the original sense, as formulated by Gray (1853: 36), the rachiglossate radula has: "teeth on lingual membrane in a single central series." A radula with "three series" was originally named hamiglossate by Gray (1853: 34). Fischer (1880-1887) has united these terms, which may cause some confusion.
[3]In the campilodont radula (terminology of Macdonald, 1869) the tooth rises from a basal plate, forming a hook together with it, whereas in the orthodont radula the tooth does not have a true basal plate and is straight. ED.

mantle cavity. An apparatus of this type must have most efficiently worked among mollusks possessing a planospiral, vertically disposed, bilaterally symmetrical shell and a dilated aperture (Fig. 1).

Mollusks possessing such shells had 2 equal and symmetrical columellar muscles, as demonstrated by the bellerophontid muscle impressions (Knight et al., 1960). The collision of 2 symmetrical water currents directed from the right and left sides in the fore part of the mantle cavity caused the development of an apparatus capable of regulating the water current. Thus the bellerophontids developed a fissure (selenizone) in the shell-wall in the middle of the mantle cavity or, in the same place, a sulcus resembling a keel when viewed from outside.

When the shell became conispiral, water regulation became a more pressing necessity.

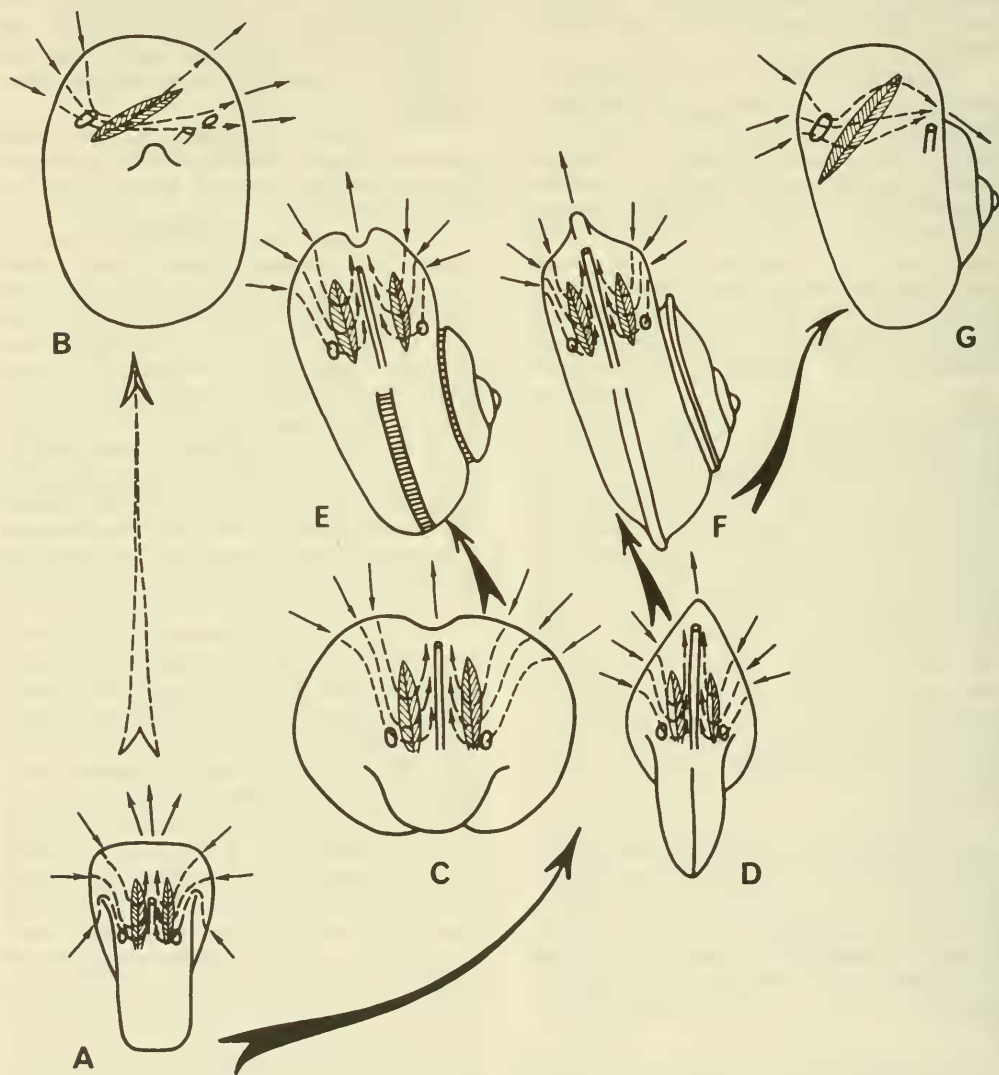There could have existed 3 principles of water regulation: 1) by means of the

FIG. 1. The location of gills, osphradia and rectums in different groups of Prosobranchia in relation to the circulation of water in the mantle cavity: A, Helcionellida; B, Docoglossa; C, D, Bellerophontoidea; E, Fissobranchia; F. Macluritida; G, Anisobranchia.

reinforcement of the fissure developed by the bellerophontids; 2) by means of sulcus reinforcement; the primarily symmetrical structure of the mantle complex, especially the paired ctenidia and osphradia, the auricles and hypobranchial glands being in both cases preserved. But, hindered by the whorls, the water current on the left side, running from the basal border of the aperture, could not be equal to that on the right side, which caused a considerable difference in the size of the ctenidia on the right and the left sides in conispiral Zygobranchia (Woodward, 1901; Bouvier & Fischer, 1902; Crofts, 1929). The kidney asymmetry of the Zygobranchia, however, is apparently not related with water regulation, being a result of the double (excretory and reproductive) function of the right kidney. It must be noted that the development of a fissure caused a more effective water current regulation than the development of a sulcus could have given, which resulted in the survival of the fissuriform species until the Recent. 3) The third principle of water-regulation regards the use of the canal formed by the palatal and parietal walls of the last whorl. When the conispiral shell has its apex turned aside upward or somewhat backward, the water can enter the mantle cavity along the basal and the greater part of the palatal borders of the aperture, while it can leave the cavity near the anus, which is placed a little backward and to the right (in dextral forms). However, the anus must be displaced towards the upper suture of the body whorl, which inevitably causes the loss of the right ctenidium and destroys the symmetry of the mantle complex.

From the above considerations we conclude that 2 groups, Zygobranchia and Anisobranchia, usually classified among Diotocardia, doubtlessly belong to different phylogenetic lines, originating from common ancestors. Zygobranchia adopted fissure-development, including the separation of their working parts from the peristome, yet keeping the mantle complex symmetric. In Anisobranchia the anus became displaced toward the suture and they developed an asymmetry of the mantle complex. The second tendency found its further development in all Monotocardia, for which reason they can be connected with Anisobranchia.

The analysis of the central nervous system of these 2 groups similarly reveals the existence of 2 phylogenetic lines. The central nervous system of the Zygobranchia lacks separate ganglia, the nerve cells being disposed along the nerve cords; only in *Fissurella*, where the nervous system is at its highest concentration, is a supraintestinal ganglion formed. On the other hand, special branchial ganglia were developed to innervate the gills that are not, strictly speaking, connected with the central nervous system, and that secure gill function by means of a special complex apparatus.

In Anisobranchia, a marked concentration of nerve cells occurs in the ganglia, which is most notably expressed in the cerebral and pleural sections, though their nervous system is but weakly concentrated. The further evolution of this tendency leads to a characteristic system of ganglia in Monotocardia.

The study of other characteristics which are usually brought forward as convincing arguments for the union of Zygobranchia and Anisobranchia does not disprove the assumption that these groups had different types of development. On the other hand, the analysis of the tendencies of the morphological peculiarities in Anisobranchia and Monotocardia supports the view that they are phylogenetically akin, the former being ancestral to the latter.

Thus, the presence of 2 kidneys in both Anisobranchia and Zygobranchia and the absence of the right kidney in Monotocardia does not invalidate a relation between Anisobranchia and Monotocardia, as the latter sometimes do have a right kidney marked by an even stronger development (e.g., in *Circulus*; see Fretter, 1956) but performing a different function, wherefore it is called "the renal gonoduct". The fact that Anisobranchia have no pallial gonoduct does not run counter to the above point of view, as formation of a gonoduct has been observed more than once, and as there are groups among Monotocardia (Thiaridae) having no pallial gonoduct, while some of the highest Anisobranchia possess a primitive pallial gonoduct (*Calliostoma*). Some Monotocardia (Litiopidae, Janthinidae) possess a more or less developed epipodium, as well as the gastric caecum characteristic of a number of Monotocardia and even of Pulmonata. The fact that Anisobranchia possess a rudimentary vestigial right auricle[4] does not disprove their kinship with

[4]The terms "right" and "left" used in reference to the organs of the mantle complex and to the muscles refer to the post-torsional state of Gastropoda.

Monotocardia, as, after careful investigation, the same can also be discovered among the highly developed representatives of Monotocardia (see Spillmann, 1905). However, it must be emphasized that several independent phylogenetic branches of Monotocardia have originated from Anisobranchia, and that, if the latter are grouped together with Zygobranchia and separated from Monotocardia, such classification must be wrong, for the reason that when different groups of Monotocardia are derived from Diotocardia as if they were independent of each other, the phylogenetic unity of the system of Prosobranchia is destroyed.

While comparing Zygobranchia to Anisobranchia we excluded Docoglossa, which are often placed in Diotocardia.

If this comparatively restricted group is set against the 2 remaining groups of Diotocardia, it should be taken into consideration that its representatives can possess a vast number of peculiarities that have no connection with their phylogenetic relationship, but that result from specialization and that developed convergently with analogous peculiarities of other groups of prosobranchs, side by side with peculiarities having a phylogenetic value.

Therefore, it is important to give a detailed analysis of the structure of all the main docoglossan organs, as compared with the rest of the Diotocardia.

All Docoglossa (except *Propilidium*) possess a cap-like shell with the apex turned forward; they have no selenizone or sulcus, which characters separate them from the forms with cap-like shells of Zygobranchia (Fissurellacea)[5] that as a rule possess either a fissure (*Emarginula*), a perforation (*Fissurella*), or a sulcus clearly visible from the inner side of the shell (e.g. *Montfortia*). The fact that a cap-like shell may be formed from the bilaterally-symmetrical planospiral shell of bellerophon-like groups and from the conispiral shell of many other groups of Gastropoda is widely known. In both cases the spiral shell should be considered a primary type (Knight et al., 1960, and other authors). The columellar muscle in cap-like forms is usually horseshoe-shaped. However,

we can obtain some data about the character and shape of the shell of the ancestors of Docoglossa. It is known that in gastropods with a conispiral shell the right columellar muscle functions alone. The horseshoe-shaped muscle of many cap-like forms has developed from this muscle. Conispiral Zygobranchia (Crofts, 1955) retain the left muscle as a rudiment, while Anisobranchia and Monotocardia have lost it. The formation of the horseshoe-shaped muscle of Docoglossa from 2 (left and right) columellar muscles, equally increasing after torsion (Crofts, 1955) doubtlessly proves that the ancestors of Docoglossa had a planospiral, bellerophon-like shell, devoid of any slit or sulcus.

A similar shell, which also had a tendency to dilate the preapertural part of the last whorl, was characteristic of the most ancient of all known Gastropoda, the correlated Cambrian families Coreospiridae and Helcionellidae. Helcionellidae had an almost cup-like shell. Probably it was "exogastric,"[6] like that of Docoglossa (Knight et al., 1960). Thus, the Bellerophontacea proper are to be regarded as a group derived from *Coreospira*-like forms, having developed after the slit or sulcus type.

By this character Coreospiridae and *Helcionella* are similar to Docoglossa, which brings them together and sets them apart from the Bellerophontacea, that developed in the direction of the Zygobranchia.

The deviation of the antero-posterior axis of the embryonic shell from that of the definitive one by an angle of about $20°$, which was observed in the development of some Patellidae (Dodd, 1957), does not necessarily prove that the ancestors of Docoglossa were conispiral; it may have been caused by the clockwise rotation of some elements of the mantle complex, which will be discussed below.

The docoglossan mantle complex, with an unpaired ctenidium and a heart displaced to the left and forward, is at first sight similar to that of Anisobranchia; however, a detailed investigation reveals that this similarity is but slight and superficial.

The most important detail of mantle

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[5]Following Recommendation 29A of the International Code of Zoological Nomenclature, the superfamily name endings have been changed to "-oidea" in the systematic part of the present work. When, however, discussing or quoting groups in the traditionally accepted sense, the customary ending "-acea" has usually been preserved.

[6]Coiled so as to extend forward over the head. ED.

complex asymmetry in Anisobranchia is represented by the reduction of the right ctenidium, which retains its position, and by the displacement of the anus, together with the nephropores, to the right.

In contrast, the asymmetry in Docoglossa results from the clockwise rotation of the ctenidium to the left by an angle of about 20°. Besides, the ctenidium-osphradium system is disrupted and the osphradia with the corresponding ganglia retain a strictly symmetrical position even after the reduction of one or even both of the ctenidia (Haller, 1894; Thiem, 1917a, b).

Consequently, the heart is displaced to the left and, after the reduction of the right ctenidium, it lies close to the base of the left ctenidium. Such an approach to the problem helps to explain the separation of the osphradia from the bases of the ctenidia in Docoglossa, which at first sight seems a paradox. Forbes' earlier observation (Forbes & Hanley, 1850) which, however, has not been verified by further investigation, that *Propilidium ancyloides* Forbes possesses 2 ctenidia, placed asymmetrically like those in *Acmaea*, would help to support our view.

The shifted position of ctenidia in Docoglossa results from the fact that the double water currents converging from 2 sides were replaced by a one-sided current, flowing from left to right. The water current along the inner border of the mantle, the site of the adaptive, secondary, mantle gills in Patellidae, is a further stage in the transformation due to the one-sided current.

The above data lead us to the conclusion that the mantle complex asymmetry in Docoglossa has developed independently from the asymmetry in Anisobranchia; the forms possessing a symmetrical mantle complex should be regarded as forms ancestral to Docoglossa. The problem as to what ancestors the forms with a one-sided water current were derived from is more difficult to solve; it is especially difficult to give details on development. However, the reason for the change in water currents should be sought in the same hydrodynamic difficulties which have caused the formation of the slit or the sulcus in Bellerophontacea.

The vascular system does not furnish sufficient evidence to enable us to expose the phylogenetic connections of Docoglossa since it is, in the main, of the same type as that of the other Diotocardia. We can only point out that the ventricle of Docoglossa is divided into 2 unequal parts; one functions as ventricle, the other is transformed into an arterial bulbus (Spillmann, 1905). This peculiarity of Docoglossa singles them out from the rest of the Prosobranchia.

The kidneys of Docoglossa are in all ways similar to those of the rest of Diotocardia. The right kidney is larger, as it has an excretive as well as a reproductive function.

However, the gonad in Docoglossa does not open into the renopericardial duct but directly into the kidney itself (Fig. 2). According to the system suggested by Pelseneer (1906) such a position would be secondary. This, however, is not convincing because Pelseneer's scheme was established for bivalve mollusks whose gonad opens into the renopericardial duct, on the basis of *Solemya* alone. Having considered this bivalve to be the most primitive of the Protobranchia, Pelseneer thought the position of the gonadal opening in that genus to be primary. At present, however, there is some cause to question whether *Solemya* is the most primitive representative of the Protobranchia. On the other hand, the monoplacophoran gonad opens directly into the kidney (Lemche & Wingstrand, 1959); moreover the gonad of *Haliotis* opens either into the kidney or into the renopericardial duct (Totzauer, 1902; Crofts, 1929) and that of *Pleurotomaria* immediately into the kidney (Woodward, 1901). Finally, the phylogenetic value of the relations between the kidney and the gonad should hardly be taken into consideration, as the kidney itself is separated from the renal-pericardic coelomic sac-like primordium in the course of development (D'Asaro, 1966) and both types of kidney and gonad connection reflect the union of the gonad with the coelom ancestral for Gastropoda. Anyhow, the difference in the character of kidney and gonad connection in Docoglossa and the majority of Prosobranchia ought to be considered proof of the peculiar line of evolution of Docoglossa.

The complicated reproductive system in Docoglossa went entirely its own way, independent of the rest of Prosobranchia. In the highest representatives (*Acmaea sybaritica* Dall, etc.) it resulted in the formation of a copulatory apparatus, which the other Diotocardia have never possessed.

The docoglossan radula is essentially different from the radula of the remaining Gastropoda because, when functioning, it
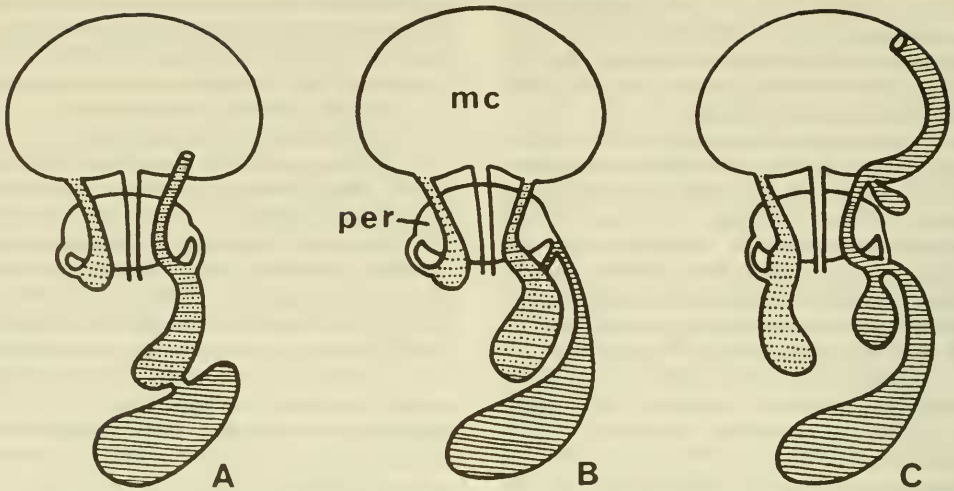
FIG. 2. The relationship between the gonad, kidney and pericardium in different groups of Prosobranchia. Organs having an excretory function are dotted, those having a reproductive function are horizontally lined; a combination of dotting and lining indicates a double function of a given organ. A, Cyclobranchia; B, Scutibranchia and lower Pectinibranchia (Anisobranchia); C, higher Pectinibranchia.

does not bend lengthwise; therefore during food-collection, each of its teeth moves only parallel to the longitudinal axis of the radula. (Its function has been described in detail by Ankel (1938).) In the remaining Prosobranchia, regardless of radular character (be it rhipidoglossate, taenioglossate, ptenoglossate or rachiglossate) and of the type of nutrition, the radula bends lengthwise, the central tooth being moved along with a slant to the axis, while the marginal teeth are drawn in an arc-shaped movement, the chords of the arcs being perpendicular to the radular axis, or at least forming a considerable angle with it (Ankel, 1938). The pulmonate radula movement is of almost the same type (Ankel, 1938) and the same applies to Opisthobranchia, though their radula differs slightly from the above type in that the radular row is only slightly differentiated into lateral and marginal teeth in the multidentate representatives, for which reason there is no marked difference in the trajectory of their movement. It is obvious that the type of radula movement in Docoglossa is more primitive than in the rest of Gastropoda; moreover, the central tooth, weakly developed in Docoglossa, becomes stronger in the course of transition of the radula to the type of movement characteristic of Gastropoda; it results in the differentiation of lateral and marginal teeth. On the other hand, a reverse transition from

rhipidoglossate to docoglossate type is hardly probable; the reasons for the longitudinal bending of the radula are obscure and the phenomenon has never been observed among any of the gastropods with cap-like shells except Docoglossa. The reduction of the central tooth cannot be explained either, the more since the necessity of having one compels Docoglossa to form a secondary "central tooth" by means of merging the 4 lateral teeth (Lepetidae). Finally, we should point out, that besides motion, the character of the docoglossan radula is strikingly similar to that of Loricata and Monoplacophora; it has much in common with the latter in its structure (Lemche & Wingstrand, 1959). In the docoglossan radula there are also some peculiarities of specialization, particularly as regards the reduction in the number of teeth and in their differentiation.

According to Graham (1949), the stomach of the initial gastropod type was divided into 2 parts: the post-oesophageal part, into which opens the hepatopancreas, and the elongated part, where the protostyle is situated. The first part is thought to have had a chitinous lining and a caecum. However, it is doubtful whether the latter was actually present. In Zygobranchia the caecum is more weakly developed than in Trochidae (Fretter & Graham, 1962).

The lowest Bivalvia, the Protobranchia (Purchon, 1956), have no marked caecum;

finally, *Neopilina* has neither a caecum nor a chitinous lining (Lemche & Wingstrand, 1959).

From these facts we conclude that the stomach of the most primitive Gastropoda had no caecum and probably no chitinous lining, or, at best, one that was but weakly developed. The Docoglossa have a stomach of such a type, divided into 2 parts, devoid of caecum and chitinous lining and with a strictly terminal entrance (Haller, 1894; Thiem, 1917a, b). The difference lies only in the absence of the protostyle within Docoglossa.

The nervous system of Docoglossa is strongly reminiscent of that of Zygobranchia. Both are characterized by a weak development of the ganglia of the pleurovisceral cord, by the presence of special branchial ganglia (which are termed the osphradial ganglia in Docoglossa), by a considerable development of the labial ganglia and of a labial commissure. However, in addition to the above-mentioned characteristics, the nervous system of Docoglossa has a very typical peculiarity. Along the mantle margin, making up a circle, run 2 ganglionic nerve cords, which are connected with the symmetrical mantle nerves (Haller, 1894; Willcox, 1898; Thiem, 1917a, b). They are especially marked in *Acmaea*, s. l., and in *Lottia*, less marked in *Cellana*, and have not yet been observed in Lepetidae. Thiele's efforts (1895) to homologize them with the pleurovisceral cords of the chitons was subjected to justified criticism (Dogel', 1940; Ivanov, 1940). We consider the attempt to explain the formation of these cords by the ganglionization of the mantle nerves unfounded. If the latter hypothesis were accepted the fact that the mantle nerve cords in Tecturidae and Lottiidae are well developed while they are not observed in the phylogenetically more advanced forms could not be explained.

The above assumption is the more dubious, as the transformation of the cords into nervous connectives devoid of ganglionic cells is a common enough fact, whereas we have no reliable evidence of the reverse process. We consider it safer to explain the formation of the mantle cords by the concentration of the nervous plexus of the mantle border, which recurs in the representatives of many groups of Prosobranchia. The peculiarity of the mantle nerve cords in *Patella* supports this point of view (Haller,

1894), as in many respects they remind one of the nerve plexus.

To sum it up, the Recent Docoglossa have many characters that are more ancestral than those of the most primitive of the existing Zygobranchia, i.e. the primarily symmetrical shell without any slit or canal, and the radula and its type of movement. Besides, they have many peculiarities in common with Zygobranchia that testify to the descent of each of these groups from common ancestors, i.e. the connection of the gonad with the kidney, the stomach structure, the character of the central nervous system, and the development of branchial and labial ganglia. Moreover, Docoglossa have some peculiarities that show that they went their own way of development: the asymmetry of the mantle complex and its structure, the specialization and the decrease in and number of radular teeth, the absence of a protostyle and the formation of mantle nerve cords. Therefore, Docoglossa should be regarded as a separate phylogenetic line, the initial members of this line being the Cambrian Coreospiridae and Helcionellidae. This line is definitely more distant from the 2 groups (Zygobranchia and Anisobranchia plus Monotocardia) discussed above, each of the latter having more in common with one another than with Docoglossa.

We wish to emphasize that separation of the subclasses is based on those general morphological characters of organization which determine the possibility or impossibility of certain concrete adaptations. Thus, to mention only a few examples, in the forms with a peripheral throw of water in the mantle cavity (Scutibranchia) one ctenidium can never completely disappear; nor can any factor prevent ctenidium disappearance in the forms with water currents as they occur in the Pectinibranchia. The variety of teeth occurring in Pectinibranchia, Opisthobranchia and Pulmonata could have developed only on the basis of a radula bending lengthwise while the unbending radula of the Cyclobranchia (as well as that of the Loricata and Monoplacophora) could never have resulted in anything of this sort.

We are convinced that the 3 main phylogenetic lines under consideration as regards the independence of their evolution (disregarding some groups among them that are not yet fully investigated) are equal in importance to those of Opisthobranchia and

Pulmonata. Pulmonata have separated at an early stage of development of the mantle complex asymmetry (i.e., when one of the ctenidia was reduced and the anus was displaced toward the parieto-palatal canal). Later this group evolved toward a general reduction of the mantle cavity and its substitution by the pulmonary cavity, which, apparently, presented a special outgrowth of the mantle cavity (Régondaud, 1961a, b; Harry, 1964).

In Opisthobranchia the original asymmetry increased as a result of the increased detorsion, whereas, when the shell was reduced, the mantle cavity followed suit.

The present data on the evolution of karyotypes in gastropods (Nishikawa, 1962; Burch, 1965, 1967; Patterson, 1967) do not contradict the above considerations. The lower forms in each subclass usually have low numbers of chromosomes, the minima in prosobranchs, opisthobranchs and pulmonates being 7-9, 12 and 16 pairs of chromosomes respectively. In the course of evolution numbers increase in parallel in different subclasses. That, for example, in Scutibranchia the minimum number of reported chromosomes is as high as 16 may be explained by the fact that only high ranking families (Haliotidae and Fissurellidae) of this subclass have been studied. At the same time high numbers of chromosomes are generally reported in the more advanced subclasses and groups, the maximal haploid chromosome numbers being, in Pectinibranchia (n = 36), in Opisthobranchia (n = 18) and in Pulmonata (n = 34-36). In cases of polyploidy, though, there occur multiples of the basic numbers (n = 60 or 72).

In our opinion the above considerations are sufficient reason for regarding the 3 phylogenetic lines under discussion here as equal in rank with Opisthobranchia and Pulmonata, i.e. justifiably to represent subclasses of the class Gastropoda. Assigning to them their oldest names, we shall give the following characteristics of each subclass.

KEY TO LETTERING ON FIGS. 2-5

|	
a	nerve anastomosis
ab	arterial bulb
an	anus
ao	aorta
asn	asymmetrical mantle nerve
au	auricle
br	branchial ganglion
c	cerebral arc/ganglion
ca	caecum of stomach
cm	columellar muscle
ct	ctenidium
e	eye
ep	epipodium
ept	epipodial tentacles
f	foot
fis	fissure of shell
frt	frontal tentacle
g	gonad
h	hepatopancreas
hg	hypobranchial gland
i	intestine
j	jaws
k	kidney
lc	labial commissure
m	mouth
mc	mantle cavity
mn	mantle nerve cords/ring
mt	free part of mantle
oe	oesophagus
oep	oesophageal pouches
op	operculum
os	osphradium
ov	oviduct
pe	penis
per	pericardium
pg	pedal nerve cord/ganglion
ph	pharynx
pl	pleural ganglion
pr	proboscis
r	rectum
rd	radula
s	shell
sb	subintestinal ganglion
sg	salivary gland
sgr	seminal groove
sip	siphonal process
sn	symmetrical mantle nerve
sph	siphon
spr	supraintestinal ganglion
sr	seminal receptacle
st	stomach
t	tentacle
ts	testis
ut	uterus
v	ventricle
vd	vas deferens
vg	visceral ganglion
z	right zygosis
♂	male orifice
♀	female orifice
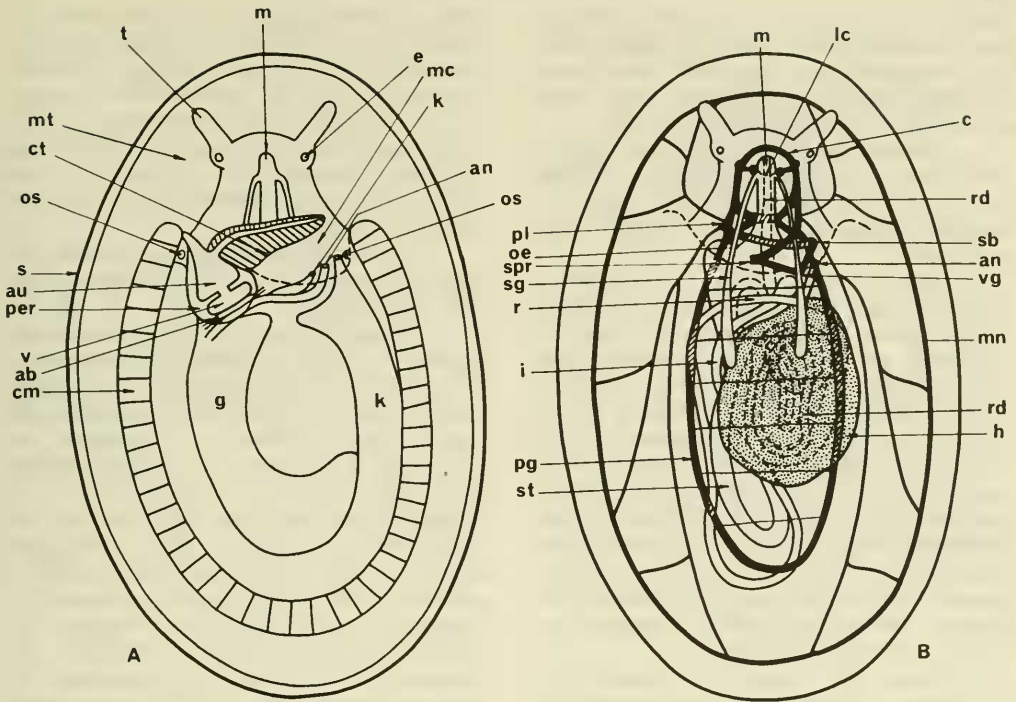
FIG. 3. General structural plan of Cyclobranchia (dorsal views).

SUBCLASS *CYCLOBRANCHIA*
CUVIER, 1817 (Fig. 3)
.

(= Helcionellacea Wenz *sensu* Knight, Batten & Yochelson, 1960 + Archinacelloidea Knight & Yochelson, 1958 + Docoglossa Troschel, 1852).

The shell is primarily symmetrical, without any incision or sulcus, planospiral, endogastric[7], or cap-like with the apex displaced anteriorly, rarely posteriorly. The head bears one pair of tentacles. The epipodium is absent. The columellar muscle is originally paired; in cap-like forms it is horseshoe-shaped and develops from 2 muscle primordia. The mantle complex is primarily symmetrical; in Recent cap-like shell forms it is asymmetrical due to the clockwise rotation of the ctenidia and sometimes on account of the presence of the left ctenidium only, of the shift of the heart to the left and of the anus with the nephropores to the right. The osphradia retain their initially symmetrical position, the right osphradium occasionally disappears, the

hypobranchial gland is absent. A circle of adaptive (secondary) mantle gills may be present. The heart has a well-developed left auricle, the right one being rudimentary; the arterial bulbus is present. There are 2 kidneys, the right kidney being larger and the gonad opening into it (not into its renopericardial duct). The reproductive system opens by a nephropore, the papilla of the right kidney sometimes continues into a long tube. Occasionally a copulatory apparatus of cephalic origin may also be present. Fertilization is mostly external. There are 2 pairs of salivary glands. The oesophagus is supplied with large sacs dilating into the gizzard. The radula is docoglossate, with many teeth in a transverse row in primitive forms, and a reduced number of teeth (6) in higher forms. When in motion the radula does not bend longitudinally and all teeth move only in one direction, coinciding with that of the movement of the whole radula. The stomach is divided into 2 parts, is devoid of protostyle, chitinous lining and caecum. In Recent forms, the rectum pene-

[7]Coiled so as to extend backward over the foot. ED.

trates the pericardium and not the ventricle. The central nervous system in higher forms has pronounced ganglia; Osphradial (branchial) ganglia and mantle nerve cords are present. There is no dialyneury.[8]

The subclass Cyclobranchia is divided into 3 orders, of which Docoglossa, with all their Recent forms, retain their generally accepted scope, but are given higher taxonomic rank.

Helcionellida, included in Tryblidiacea (= present class Monoplacophora) by Wenz (1938) and in Bellerophontida by Knight et al. (1960), are regarded as a separate order of Cyclobranchia. For the absence of the fissure on the shell in this Cambrian group, on the one hand, and the absence of any traces of metameric position of the internal organs, on the other hand, do not permit assignment to either Monoplacophora or Bellerophontida. However, a marked tendency towards reduction of the spire and a forward bend of the apex in the representatives of this group make it possible to include it in Cyclobranchia.

Taking into account the absence of any visible metamery in the muscles of *Archinacella* and similar forms, and the fact that at the apical end the muscular impression lies very close to the edge of the shell, leaving no place for the head, we consider the apical end of the shell to be their posterior, not anterior, end. It is a highly distinctive feature of Archinacellidae which obviously differentiates them from Monoplacophora, where they are usually placed (Knight & Yochelson, 1960; Horný, 1963a). That the contrapical portion of the shell in *Archinacellopsis patelliformis* (Hall) has 2 separate impressions which may be considered as impressions of radular muscles, furnishes further support for our view, already expressed in a recent study on the systematics of Monoplacophora (Starobogatov, 1970). The radulae of docoglossan type (in Monoplacophora and lower Gastro-

poda) are moved by a very strong system of muscles. The strongest of these, in Monoplacophora, are long radular muscles attached to the shell near the anterior edge of the muscular ring. Acmaeidae (= Tecturidae) and Patellidae have similar muscles, but their impressions are fused with the anterior ends of the horseshoe impression of columellar muscles.

For the above reasons we include the order Archinacellida in the gastropod subclass Cyclobranchia.

The evolution within Cyclobranchia, which proceeded in parallel to that in Scutibranchia, shows a tendency towards a smaller shell (with the average shell-length ranging from 55 mm in Patelloidea to 15 mm in Lepetoidea)[9], a less sculptured shell, oligomerization of the radula, manifested by fewer teeth per transverse row, the reduction of the specialized breathing organs, a larger renal papilla that began to protrude, the formation of a copulatory apparatus and a consequent transition to internal fertilization and ovoviviparity. The number of living species in Cyclobranchia does not exceed 350, of which only about 20 species belong to the phylogenetically youngest superfamily Lepetoidea. The most primitive of the recent representatives of the subclass live in the Indo-West-Pacific biogeographical region (about 120 species). Phylogenetically young representatives of the superfamily Tecturoidea and the majority of species of Lepetoidea are abundant in boreal waters (about 90 species). In the intertidal zone and in the extreme upper part of the sublittoral zone, i.e. on stony and rocky bottoms, the subclass shows the widest diversity of forms and the largest number of representatives. They live a semi-mobile life, feed on seasonal macrophyta and microphyta, scraping them off stones, and rarely on detritus. They appear to be mostly protandrous hermaphrodites.[10]

[8]Special arrangement of the nervous system with anastomosis of the pallial and visceral nerves, as in *Haliotis*. ED.

[9]The sizes of gastropod shells given here and later for different groups are based on an analysis of a total of over 20,000 dimensions, in part culled from the literature (Tryon & Pilsbry, 1880-1890; Philippi, Küster, Kobelt, Weinkauff, Clessin and Thiele, all in Martini & Chemnitz, 1846-1912) and in part from measurements from the collections of the Zoological Institute of the Academy of Science of the U.S.S.R. in Leningrad.

[10]At least there is no evidence for bisexuality in the Docoglossa, while there exist many records of protandry in representatives of this group (Willcox, 1898; Orton, 1920; Thorson, 1935, Bacci, 1948; Pellegrini, 1948; and others). Tecturidae, including *Acmaea*, are without exception hermaphrodites, as is also *Bathysciadium*. Consequently, until proof to the contrary is produced, we may assume that all Cyclobranchia are hermaphrodites.
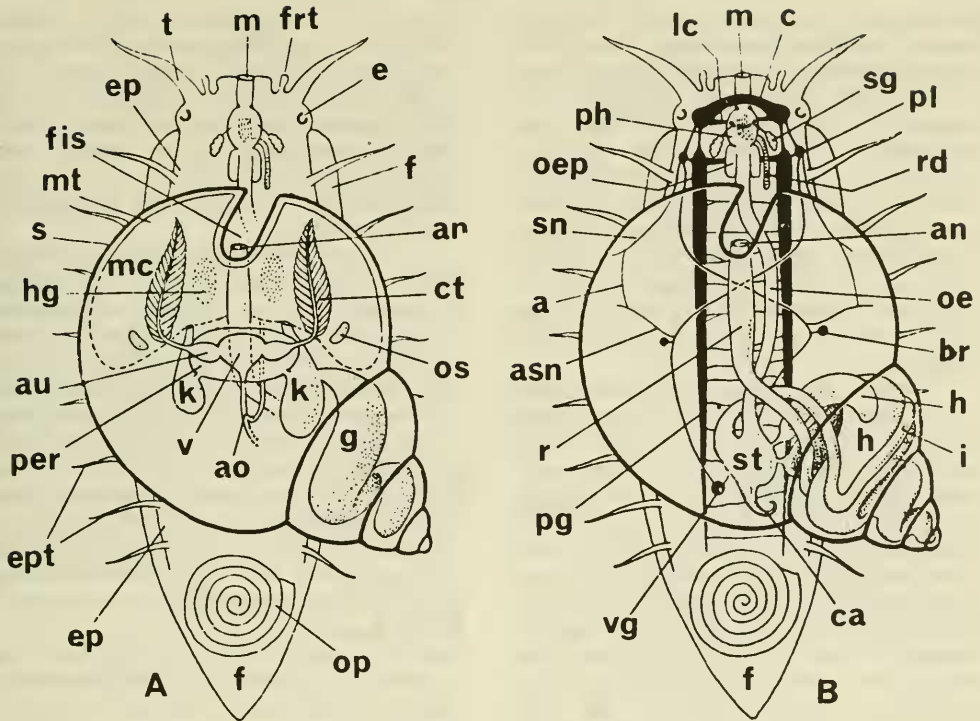
FIG. 4. General structural plan of Scutibranchia (from Ivanov, 1940).

SUBCLASS *SCUTIBRANCHIA*
CUVIER, 1817 (Fig. 4)

(= Bellerophontina Ulrich & Scofield, 1897, excluding Helcionellacea + Zygobranchia Spengel, 1881)

The shell is either primarily symmetrical, planospiral, endogastric, often of a cap-like form, or conispiral; on the anterior periphery of the last whorl above the head there is always either an incision or a sulcus that appears as a peripheral keel when viewed from outside. In the course of growth, the incision may separate from the peristome, i.e. close to form a foramen and be displaced; in cap-like forms the foramen may become apical. The head has one pair of tentacles. The epipodium is well developed and is usually supplied with tentacles. The columellar muscle is paired; in primarily symmetrical planospiral forms the right and left muscles are equal; in cap-like forms they merge posteriorly to form a single horse-shoe-shaped muscle. In conispiral forms the left muscle is rudimentary, while the right

muscle is well developed. The mantle complex is symmetrical, except that the right kidney is somewhat larger than the left. There are always 2 ctenidia in conispiral forms, the left always being larger than the right. The gonad opens into the right reno-pericardial duct and rarely into the right kidney. A copulatory apparatus is always absent. Fertilization is external. There is one pair of small salivary glands, located in the head. The oesophagus has a pair of oeso-phageal pouches. The rhipidoglossate radula is supplied with a great number of teeth, and, when in motion, is bent longitudinally with all its teeth moving in various directions that, except for the rachidian tooth, do not coincide with the direction of radula movement. The stomach has a caecum, a proto-style, and a chitinous lining. The rectum runs through the pericardium and the ventricle. The central nervous system has no prominent ganglia. Branchial ganglia are present, but no mantle nerve cords.

The subclass Scutibranchia is divided into 3 orders: Dicranobranchia, Fisso-branchia and Macluritida, having different

shell characters, different times of origin and probably different anatomies. The order Dicranobranchia, which came into existence in the early Cambrian, includes the superfamily Bellerophontoidea and the superfamily Fissurelloidea. We think it reasonable to unite in one group the plano-spiral Bellerophontoidea, which became extinct in the Triassic, and the limpet-shaped Fissurelloidea, which appeared at that time, in particular if we take into account that the development of the latter group does not show any trace of a conispiral shell in their ancestors.

Besides, the presence in Fissurelloidea of a cap-like shell with a horseshoe-shaped columellar muscle developing from nearly equal rudiments (Crofts, 1955), its usual symmetry, and similarities in the location and size of the mantle complex, together with various progressive features in the structure of the nervous system, provide good reason to consider this group as derived from Bel-lerophontoidea, which had a planospiral endogastric shell. The Fissurelloidea are thought to continue the line of bel-lerophontid evolution side by side with Fissobranchia, which in the course of their evolution developed a conispiral shell and separated from bellerophon-like ancestors much earlier. That we find no noticeable transition between cap-like and Recent conispiral forms of Scutibranchia provides additional evidence in favor of this view. The order Fissobranchia, which is phyl-ogenetically related to the Dicranobranchia, followed an independent line of evolution, due to the formation of the conispiral shell, while the symmetrical plan of structure of the mantle complex remained similar in the 2 orders. In general the scope of this order coincides with that of the superfamily Pleurotomariacea of other authors; the few modifications made are only within the order itself (see the notes).

The third order, Macluritida, that became extinct in the Triassic, exhibits a special line of evolution in the Scuti-branchia. Its characteristic feature was a tendency to develop a depressed sulcus or a process instead of a fissure (selenizone) on the body whorl. This order may be con-sidered ancestral to the subclass Pectini-branchia, the most primitive representatives of which could derive from Macluritidae or from their common ancestors. It is possible that the families of this order should be grouped in 2 independent orders: Maclu-ritida, with a pseudosinistral shell (including the sole superfamily Macluritoidea), and Trochonematida, with a normal, dextral shell (including the remaining superfamilies). Such a classification would follow from Minichev & Starobogatov's (1971) con-siderations on the origin and evolution of heterostrophy.

To sum up the trends in the Scuti-branchia: the evolution of this old subclass of Cambrian origin showed a tendency towards a smaller shell—in Recent forms the average height of shells vary (see foot-note 9) from 91 mm in Pleurotomarioidea and Haliotoidea to 24 mm in Fissurelloidea; secondary reduction of the degree of shell coiling; less pronounced spiral sculpture (see footnote 12) and more prominent axial sculpture; further, as already stated, separa-tion and displacement of the fissure from the peristome, the fissure itself growing smaller; and a larger right kidney serving a double function.

The number of Recent species of the subclass Scutibranchia does not exceed 450. More than half of them belong to the phylo-genetically youngest superfamily Fissurel-loidea. More than 43% of Recent repre-sentatives of the subclass live within the Indo-West-Pacific biogeographical region, which was not only the center of their evolu-tion, but also that of their origin (see foot-note 13). This idea is supported by the fact that the larger part of the superfamily Pleurotomarioidea, which is the most primitive of the Recent forms, live in the Indo-West-Pacific region (more than 68% of the species), while the superfamily Fissurel-loidea, which is phylogenetically younger, is represented there by only 36% of its species.

The mollusks of this subclass live mostly in shallow waters on hard bottoms. They feed on algae and more rarely detritus. They are bisexual, and their pelagic larvae are a prominent feature in the course of development.

SUBCLASS *PECTINIBRANCHIA* BLAINVILLE, 1814 (Fig. 5)

(= Anisobranchia v. Ihering, 1876 + Monotocardia Mörch, 1865)

The shell is initially conispiral, some-times with a secondary simplification, cap-like, tube-like or planospiral, always without
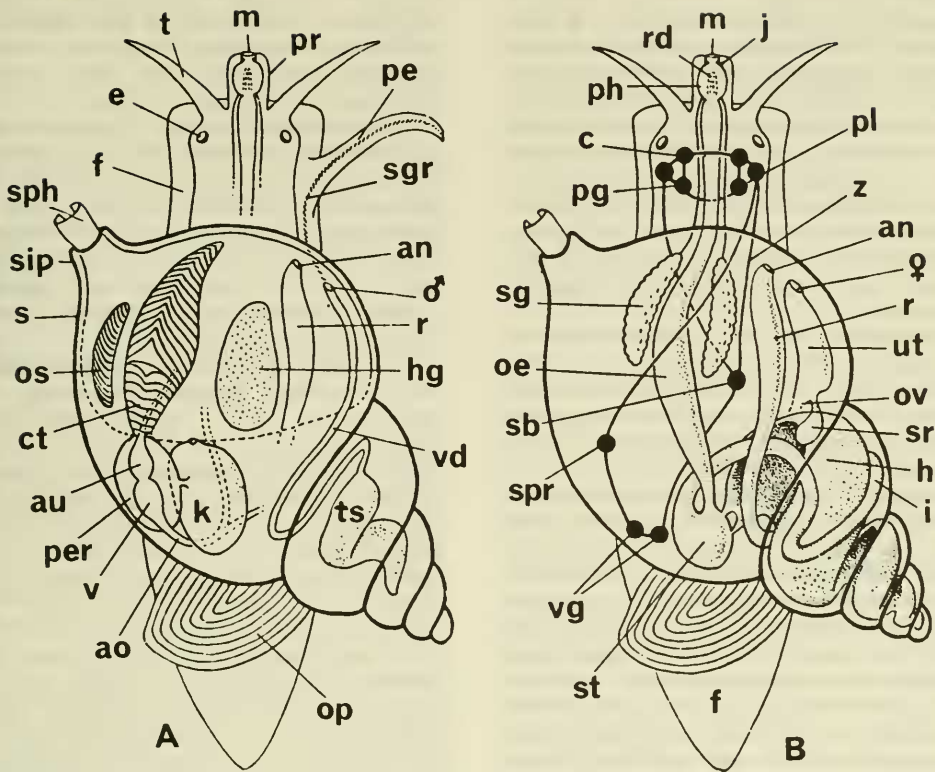
FIG. 5. General structural plan of Pectinibranchia (from Ivanov, 1940).

an incision. The head bears one pair of tentacles and sometimes has one pair of frontal lobes. The epipodium is only slightly developed, often completely absent. Only the right columellar muscle is present (in sinistral forms only the left). The horseshoe-shaped columellar muscle of cap-like forms develops from one muscle primordium. The mantle complex is sharply asymmetrical. The ctenidium and osphradium are unpaired (on the left in dextral forms). The hypobranchial glands are paired (very unequal), or more often single. Only one auricle is functional, corresponding to the only ctenidium; the other is rudimentary or completely invisible. There are 2 kidneys of which the right kidney (in dextral forms) is larger than the left, the gonad opening into the renopericardial duct; or the kidney may be completely incorporated in the reproductive system as the renal gonoduct. The reproductive system debouches either by the nephropore or continues further into the pallial gonoduct; a copulatory apparatus may also be present, arising either from the head or the foot. Fertilization is external or, more often, internal. There are 1 or 2 pairs of salivary glands; they are mostly large and situated behind the nerve ring. The oesophagus may have paired pouches, but, more often, lacks them. The radula is bent longitudinally when in action; it may be rhipidoglossate, consisting of a large number of rather homogeneous teeth, or it may have a smaller number of teeth per transverse row (7, 3, 2 or even 1). The stomach is with or without the caecum, and often has a protostyle or crystalline style. The rectum either penetrates the pericardium and the ventricle, or runs at a distance from these organs. The central nervous system has well developed and well pronounced ganglia. The lowest forms have the left branchial ganglion and show dialyneury, features absent in the highest forms. There are no mantle nerve cords.

The subclass is divided into 18 orders, characterized by a distinct structure of the shell, foot, mouth organs, gill, central nervous system, reproductive system and

distinctive ecology, the structural plan and direction of evolution being, in general, similar in all the orders. We shall not give a detailed analysis of all the characteristic features of each order, as the morphological and biological properties of their taxonomic representatives have already been given due and extensive consideration in the literature. We shall restrict the discussion of our classification only to those orders or parts of orders whose contents or position has been changed from that in the latest phylogenetic schemes.

Within the large subclass Pectinibranchia we may distinguish several phylogenetic branches, most comprising a few orders. All of them may have originated from the lowest Anisobranchia, which became extremely diversified in the Paleozoic. Each of these branches shows an independent development of the pallial gonoduct (as evidenced by the forms without a pallial gonoduct or at least by those with a longitudinally open pallial gonoduct in all the lines of evolution mentioned); they also show a concentration of the pedal nerve cords in the pedal ganglia and a change of the number of teeth per transverse row of the radula. There are 6 such phylogenetic branches for which we establish 6 superorders. Next to the superorder Turbinimorpha, which was ancestral to all the other groups and which includes only the order Anisobranchia and tentatively Lepetellida, we distinguish the following superorders: Neritimorpha (in content equal to the old superfamily Neritacea), Paludinimorpha (Architaenioglossa and probably Valvatacea), Pyramidellimorpha (heterostrophic forms together with Eulimacea and Ptenoglossa), Cerithiimorpha (Cerithiacea together with Stenoglossa = Hamiglossa and Toxoglossa, derived from them), and Littorinimorpha, comprising all the remaining groups, and considered as arising from forms that share many structural features with Turritellidae.

The ancestral order Anisobranchia, which is the most primitive in the subclass, retains its generally accepted scope with only minor modifications. The representatives of the order may have originated from old Scutibranchia as early as the Ordovician, and already by the Triassic had developed a great diversity of forms. Tentatively we here include the small order Lepetellida, following Moskalev (1971). However, its position and origin remain obscure and need further research.

Neritidae and related groups, forming a separate order Planilabiata in our scheme, show an independent line of evolution. The characteristic feature of this old order of supposedly Devonian origin is the relative complexity of its reproductive system, especially when contrasted with certain primitive elements in the structure of some other organs.

Viviparoidea and Cyclophoroidea, which may have appeared as early as the Carboniferous, form a special order Architaenioglossa. In the course of their evolution they adapted from marine life to that in fresh water and finally on land. The transition resulted in a longitudinally divided mantle cavity, in the reduction of the pectinate ctenidium and in the change from a ciliary semi-filtration type of feeding[11] to phytophagy and detritophagy.

The combination of progressive and primitive structural features and the presence of a bipectinate ctenidium freely protruding from the mantle cavity, features not observed in other Pectinibranchia, provide reason to separate the fresh-water Valvatoidea and possibly the marine Tornoidea in the special order Ectobranchia.

Turritelloidea and Vermetoidea, sharing some primitive structural features, and being an ancient, sufficiently specialized group of possibly Devonian origin, are placed in the separate order Protopoda. The characteristic features of these mollusks, which possibly might have been the ancestors of some other higher groups of Prosobranchia, are the absence of copulatory organs, the open pallial gonoduct, the elongated shell and semi-filtration feeding.

Littorinacea and Rissoacea in the generally accepted sense form one of the largest groups of prosobranchs, not only on account of the diversity of species with a distinctive morphology, but also because of their wide occurrence in shallow seas. They may be collected in one order, Discopoda, on the grounds of various common morphological features (such as a small shell with an esiphonate aperture, a rather complex repro-

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[11]Ciliary semi-filtration feeding is the ability of prosobranchs to catch the seston carried over the surface of the bottom by the ctenidial cilia and to swallow it, agglutinating the organic particles with mucus.

ductive system, an alimentary system with a taenioglossate radula, which is in general similar in the 2 groups) and a uniform direction of evolution. They were specialized, mainly phytophagous gastropods which adapted to life on plants, colonized brackish and fresh waters and later dry land. The group is not ancestral to prosobranchs of other lines of evolution. It may have originated in the Triassic, its most probable ancestors being ancient Protopoda or some progenitors common to both. Taxonomically and morphologically, Discopoda have not been studied adequately because of their small size and diversity of form, and our classification of the order may need some corrections.

The group of families generally brought together to form the superfamily Strombacea has its own collateral line in the evolution of prosobranchs. Distinct from other Gastropoda having a taenioglossate radula, Strombacea have a peculiar shell, usually with processes, a divided foot with a metapodium, an operculum with a terminal nucleus and a distinctive structure of the radula and of the reproductive system. We think it reasonable to separate Strombacea in a special order Alata. The group probably originated at the juncture of the Triassic and Jurassic, from Protopoda or some common ancestor. Of great importance for the formation of the order was the adaptation of its representatives to life on soft bottoms in the marine epifauna; it resulted in the development of different types of shell processes to keep the shell on the surface of the bottom, and in the transition to active feeding on detritus.

Raising the Heteropoda—which in the course of their evolution assumed a planktonic way of life, with all the necessary adaptations—to the rank of an order appears reasonable and needs no additional comment.

The families Cymatiidae, Colubrariidae and Bursidae (= Ranellidae) are assembled in the superfamily Cymatioidea because of similar shells and morphology. Cassididae, Tonnidae and Ficidae (assembled in the superfamily Cassidoidea) form a special group of prosobranchs. This group of Cretaceous origin arose as an independent branch of evolution, and is probably phylogenetically connected with Protopoda or Alata. Development in this group was con-

ditioned by the transition to (1) predation with the same taenioglossate radula, and (2) to a burrowing way of life. This independent direction of evolution, a characteristic shell, which is supplied with a siphonal canal, and the specific structure of the mantle and alimentary system make it possible to unite Cymatioidea and Cassidoidea in a special order Canalifera.

The superfamilies Vanicoroidea, Calyptraeoidea, Pedicularioidea, Cypraeoidea and Lamellarioidea, which mostly developed characteristic pelagic larvae, such as echinospirae, also show a special path of evolution. They have some morphological features in common and are combined in a special order Echinospirida. This large and complex group of mollusks may have appeared in the Triassic. Phylogenetically it is connected with the order Protopoda; in the course of its evolution it changed from a semi-filtration type of feeding to ectoparasitism (Vanicoroidea and Calyptraeoidea) or to predation (Cypraeoidea, Pedicularioidea and Lamellarioidea). Further characteristic features of the order are: a tendency towards reduction of the operculum; looser coiling of the whorls, resulting even in cap-like or ear-like shells; overgrowth of the shell by the mantle, resulting in complete disappearance of the external shell, or in the development of a thick, skin-like periostracum.

Phylogenetically closely connected with the above order are Naticacea, which may have appeared in the Triassic, and which developed independently as specialized predators. Naticacea are separated in a special order Aspidophora on the basis of an independent phylogenetic line of evolution, of having a distinctive shell, a propodium and a system of water-bearing vessels in the foot, and a special structure of the alimentary system (radula, acrembolic proboscis supplied with a drilling gland) and of the reproductive system.

Cerithiacea show an independent line of evolution in the Pectinibranchia. They may have appeared in the Triassic and, being a most productive group, they may have given rise to higher prosobranchs. The characteristic elongated shell with its tendency to develop a siphonal process, the operculum with its central nucleus, the character of the taenioglossate radula which shows a great variety of tooth form within this group, and

the absence of a copulatory apparatus make us separate Cerithiacea in the independent order Entomostoma.

The highest prosobranchs, which are generally brought together to make up the superfamilies Fasciolariacea, Buccinacea, Volutacea and Muricacea are in close and immediate phylogenetic relationship with the Entomostoma. This group of families, which probably appeared in the Cretaceous period, rapidly developed from detritophagy and saprophagy to specialized predation within a relatively short geological period of time. Apparently this transition brought about some reconstruction of the alimentary system, such as development of the oesophageal gland and the formation of the stenoglossan (rachiglossate) radula, with subsequent further oligomerization within the group, the development of the siphonal canal, which was always well pronounced, and the isolation of the reproductive system from the mantle cavity and the kidney. As far as the classification under discussion is concerned, the separation of this group of families in an independent order named Hamiglossa on the basis of priority needs no further consideration. It may be pointed out that Triphoridae, which show a kind of transitional link between Entomostoma and Hamiglossa, have a polydontous radula and are assigned to the suborder Rhiniglossa, and are the most primitive family in the order. The most progressive families are those in Muricoidea, which are equipped with the radula of a perfect predator, and in Cancellarioidea, with their tendency towards complete reduction of the radula. These are placed in the suborder Nematoglossa. Some further details about the order Hamiglossa are given in the notes.

Parallel to Hamiglossa there appeared a group of families usually united in the superfamily Conacea, which had the same Cretaceous origin and stemmed from the same ancestors. The characteristics of their external and internal morphology, the peculiar character of their development and the independent direction of their evolution provide sufficient reason for separating this group as a special order Toxoglossa. This order, consisting of specialized predators only, showed an evolutionary tendency towards oligomerization of the radula. The reduction proceeded parallel to, but unlike that in Hamiglossa, manifesting itself in a gradual disappearance of the rachidian tooth and of the middle lateral and marginal teeth, but not in the reduction and simplification of the lateral teeth. The most primitive families in the order, close to the lowest Hamiglossa are: Mitridae, Speightiidae, Thatcheriidae and Clavidae; the most advanced are Raphitomidae, Conidae and Terebridae.

The group of prosobranch gastropods which is generally comprised in the superfamilies Loxonematacea, Nerineacea, Pyramidellacea, Architectonicacea, Epitoniacea and Eulimacea, have an independent and distinctive line of evolution in the subclass Pectinibranchia. The morphological originality of this group, frequently mentioned in the literature, as well as the presence of heterostrophy in a number of its representatives, lead us to assume that its origin might be independent from that of the remaining Pectinibranchia. It is probable that, in the future, this group will be set apart as an independent subclass; but, for the time being, solely the reflections on the origin of heterostrophy (Minichev & Starobogatov, 1971) speak in favor of this assumption. We therefore refrain from categorical statements on this point and retain this group in Pectinibranchia. The group appeared as early as the late Cambrian or Ordovician, when differentiation of Pectinibranchia into orders was just starting. The group might have developed from common ancestors with Anisobranchia or even Opisthobranchia and Pulmonata. It is divided into a number of orders at different levels of evolution and specialization within the new superorder Pyramidellimorpha. The main trend in the evolution of these mollusks was the transition from free life and predation to commensalism, ectoparasitism and further to endoparasitism. Morphologically it gradually led to a smaller and reduced shell and radula, a more complex reproductive system, accompanied by an increased sexual dimorphism. The independence of the evolutionary line of this group is supported by a peculiar multidentate, weakly differentiated radula transitional between the campylodont and orthodont type in some representatives, while in others it is fully orthodont. This type of radular apparatus could develop only from the primitive multidentate radula. Loxonematacea (which probably are connected with Subulitacea) together with Pyramidellacea, Nerineacea and Architec-

tonicacea, which phylogenetically go back to Loxonematacea, are the oldest superfamilies of the group. Heterostrophy, perhaps a characteristic feature of primary forms which may have disappeared in some groups, a peculiar shell, an evolutionary tendency towards commensalism and ectoparasitism, and some common anatomical features, lead us to separate these superfamilies in a special order Heterostropha, with Subulitina, Entomotaeniata and Gymnoglossa as its suborders. The taxonomic position of Pyramidellacea, which are occasionally included in Opisthobranchia (Fretter & Graham, 1962) has caused many disputes and discussions. In our opinion the direct phylogenetic connection of Pyramidellacea with the above mentioned extinct mollusks, as well as with Architectonicacea, and of the latter group with Epitoniacea, contradict these views.

Epitoniacea and Janthinacea, which in the course of their evolution adapted to pelagic life, form a special group of gastropods that may have appeared at the juncture of the Triassic and Jurassic and developed from some ancestors held in common with Gymnoglossa. The character of the shell, the presence of the ptenoglossate radula in all the representatives, the absence of heterostrophy and the apparent evolutionary trends make it possible to unite these superfamilies in a special order Ptenoglossa.

Eulimacea (= Melanellacea), which are phylogenetically connected with the line of Subulitacea-Loxonematacea, are the most specialized group of the branch under consideration. These mollusks, lacking a radula and showing considerable morphological changes caused by the transition from commensalism and ectoparasitism to endoparasitism, are separated in the order Homoeostropha.

The evolution of the phylogenetic branches in the subclass Pectinibranchia had many features in common, which was often expressed by parallelism in each of the above mentioned phylogenetic branches. We observe: a common tendency towards weakening of shell sculpture in general and of the spiral sculpture in particular[12]; the formation, very often quite independently, of

the siphonal process; disappearance of the epipodium; reduction of jaws; oligomerization of the radula, which took different forms in different groups and often led to its complete reduction in specialized mollusks; a more pronounced asymmetry of the mantle complex; formation of the pectinate ctenidium, attached to the mantle, and of the pectinate osphradium; transformation of the right kidney remnants into the renal gonoduct; formation and development of the pallial gonoduct and of the copulatory apparatus; concentration and integration of the central nervous system. The Pectinibranchia, which are the most highly developed subclass among Gastropoda, consist of about 12,000 Recent species. The 3 orders with the largest number of species are: the Anisobranchia (about 1,500), which are almost solely responsible for the diversity of the groups of the subclass, and the relatively young and phylogenetically advanced Hamiglossa and Toxoglossa (about 2,000 and 3,000 species respectively). More than half of the total number of species lives in the Indo-West-Pacific biogeographical region, which was the source of the high variety of forms of the subclass. As the most primitive representatives are also among them, this region was probably its center of origin[13]. This assumption is also supported by the fact that about 60% of all the Recent species of Anisobranchia and about 70% of Planilabiata live in tropical waters in the western part of the Pacific Ocean. The region of the present Mediterranean Sea and adjacent waters may also be considered to be an old center of form-building and evolution of the subclass Pectinibranchia. But that region is not so rich in forms and only about 20% of all species of the subclass live there now. The number of species of this subclass is about equal in all other biogeographical regions.

In temperate and cold waters only the highest of the phylogenetic lines discussed developed a considerable diversity of forms. The most developed are the species of the orders Echinospirida (about 90 species, i.e. about 36% of the total number of species of this group) and Hamiglossa (about 200

[12]The primary nature and great primitiveness of spiral sculptural elements of the gastropod shell have been well shown by Grabau (1928). From published data and from our own observations we could observe a decrease of spiral sculpture coupled with a relatively greater prominence of axial sculpture not only in phylogenesis but also in ontogenesis of pectinibranchs.
[13]This view is shared by a number of biogeographers, among them Ekman (1953); it applies also to crabs (Stephenson, 1962) and other groups of animals.

species, i.e. about 18% of the total for this group).

As to their biotopic preferences, the representatives of all the phylogenetic branches of the subclass exchanged, in the course of their evolution, rocky bottoms of shallow waters (the initial habitat of gastropods) for submerged plants, the open sea, epifauna of semi-hard bottoms and lastly for soft bottoms, migrating occasionally into the infauna; they also changed shallow water habitats for the deep sea and abyssal waters, and for fresh water and dry land. In fact, the majority of the representatives of the most primitive ancestral order Anisobranchia live on rocky bottoms in shallow waters, as also do the majority of species of the old order Planilabiata. They inhabit wide expanses of the littoral zone in tropical and subtropical latitudes, sometimes brackish and occasionally fresh waters. The species of the orders Architaenioglossa and Ectobranchia, which appeared in late Carboniferous or early Triassic times, live in fresh waters and on dry land. The species of the relatively old order Protopoda live mainly on hard, sandy, stony or rocky bottoms in shallow waters, while the younger orders Discopoda, Alata, Heteropoda, Canalifera, Echinospirida and Aspidophora, which are phylogenetically connected with Protopoda, inhabit vegetation such as leaves of underwater higher plants and thalli of algae, epifauna of semihard or soft bottoms, infauna, and pelagic communities. The phylogenetically youngest and highest orders Hamiglossa and Toxoglossa have the relatively highest percentages of species living in waters of considerable depth, on soft bottoms and in the infauna.

As for the type of feeding, the subclass clearly shows a tendency, parallel in different phylogenetic lines, of transition from initial microphagy, sestonophagy and phytophagy (in the majority of species of the orders Anisobranchia, Planilabiata, Architaenioglossa, Ectobranchia, Protopoda, Discopoda and Entomostoma) to detritophagy, saprophagy and predation (in the majority of representatives of the orders Alata, Heteropoda, Canalifera, Echinospirida, Aspidophora, Hamiglossa, Toxoglossa and Ptenoglossa). In the orders Heterostropha and Homoeostropha parasitism evolved and with it a special suctorial type of feeding.

Reproduction changed from external to internal fertilization; then, on account of a shortened pelagic stage, to the formation of egg capsules, to direct development and ovoviviparity.

The size of the shell, its change, and the direction of that change, are closely connected with the peculiarities of the ecology of a group in general and its type of feeding in particular. On the whole, in the course of its evolution, the subclass shows a tendency towards a larger shell because of the dominance of saprophages and predators at the top of different parallel evolutionary lines. The mean height of the shell (see footnote 9) in the ancestral order Anisobranchia is 18 mm, while in the phylogenetically younger orders Aspidophora and Alata it is 26 and 90 mm respectively in one line of evolution and, in another line of evolution, in the most advanced groups of the subclass, i.e. the orders Hamiglossa and Toxoglossa, it is 40 and 28 mm respectively. Nevertheless the evolution of phytophagous forms showed a tendency towards a considerably smaller shell, while microphagous and sestonophagous forms showed almost no change, or tended towards a slightly larger shell. In the line of evolution Anisobranchia-Protopoda-Discopoda the mean height of the shell varies from 18 mm in the ancestral phytophagous group to 35 mm in sestonophagous Protopoda, and to 6 mm in phytophagous Discopoda. Within the last order the mean height of the shell changes from 10 mm in the superfamily Littorinoidea to 4 mm in the phylogenetically advanced superfamily Truncatelloidea. It should be noted, however, that in the course of their evolution predators and saprophages, which are in general larger than phytophages and sestonophages, within certain limits also show a tendency towards a smaller shell. In the order Hamiglossa, for example, the suborder Rhiniglossa has the smallest shell (the mean height of the shell being 10 mm), and Rachiglossa the largest (40 mm). Nematoglossa, being a phylogenetically younger group, show secondary diminishing of shell size (28 mm).

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It is interesting to note that all 3 subclasses under consideration show much similarity in phylogeny and evolutionary trends. This similarity is revealed in parallel

evolutionary tendencies towards: more pro-
nounced asymmetry and oligomerization of
the radula; a more complex reproductive
system, connected with the transition from
external to internal fertilization, and from
possessing a pelagic larva to direct develop-
ment and ovoviviparity; also, the concentra-
tion and integration of the central nervous
system. However, as has already been shown
in the present paper, similar evolutionary
problems were solved in different ways in
the different subclasses, and results have not
always been equally successful. It should be
stressed here that convergence never involves
those main morphological features that
make the subclasses in question different
from each other. Thus, in spite of the fact
that limpet-like forms, which often had
similar ways of life and similar manners of
feeding, very often appeared in different
subclasses, their internal morphology reflects
the main morphological features of the
corresponding subclasses. For example, the
shape and function of the radula and some
other peculiar structural features of Cyclo-
branchia differ very greatly from those in
the cap-like forms of Scutibranchia and
Pectinibranchia in spite of the similarity in
their ecology, of the external shape of the
shell and of the columellar muscle. The
cap-like forms of Scutibranchia and Pectini-
branchia are also very dissimilar morpho-
logically, though the function of their
radulae is in general the same. The above
reflections support the evolutionary inde-
pendence of the subclasses in question. The
distribution of Recent species in the sub-
classes is in agreement with a well-known
phylogenetic tendency for an increase in the
number of species in phylogenetically ad-
vanced groups. Thus, the lowest number of
species is found in the most archaic gastro-
pods (Cyclobranchia) and the highest in the
most progressive groups (Pectinibranchia,
Opisthobranchia and Pulmonata).

In terms of ecology and distribution,
the evolutionary parallelism in the subclasses
finds its expression in: the transition from
living on hard bottoms in shallow waters to
living on mixed and soft bottoms at greater
depths; in the change of the mode of
feeding, i.e. in the transition from micro-
phagy and phytophagy to detritophagy (in
older groups) and to saprophagy and pre-
dation (in phylogenetically younger groups);
in the extension of distribution from
tropical and subtropical waters to temperate
and cold regions; in an increase in the
number of Recent species in the phylo-
genetically youngest groups. The tempo of
form-building in the various phylogenetic
groups of Gastropoda has been uneven. This
observation is in agreement with the data on
the evolution of other organisms. The form-
building process was most active in the
Cambrian-Ordovician, Permian-Triassic and
Cretaceous-Paleogene, i.e. in the periods of
increased tectonic alterations of the earth's
crust and intensive changes of the planet's
climate.

The parallelism in the evolutionary
trends in various groups of prosobranchs is
indicative not so much of phylogenetic
relationship of the developing groups but
rather of certain common traits of evolution
then in progress that were closely connected
with physical and chemical changes taking
place in the course of the development of
our planet.

The above considerations on the evolu-
tion of prosobranchs and on its main lines
and the phylogenetic relationships between
the different groups are reflected in the
scheme of evolution and phylogeny pre-
sented here (Fig. 6) and in the subclasses,
superorders, orders, suborders, superfamilies
and families[14], listed below in their evolu-
tionary sequence.

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[14]It will be seen that a number of taxa have been elevated in rank and that a larger number of families are
recognized, as we believe that the differences between the new and old families are in no case less than
those met in the families generally accepted. By way of example, **Tibiidae** and Strombidae differ no less
than Nassariidae and Buccinidae, or Buccinidae and Neptuneidae. Still more considerable are the
differences between Pyramidellidae and Turbonillidae; in fact, the latter do not seem to be uniform and
should probably be split into Turbonillidae and Odostomiidae as the differences in the glands of the
reproductive system are as great as those between Planorbidae and Lymnaeidae. As regards the new
family **Hemitomidae**, we find the differences from Emarginulidae and Fissurellidae important and our
reasoning on the evolution of the Scutibranchia leads us to the conclusion that the Hemitomidae
originated from other bellerophon-like ancestors.
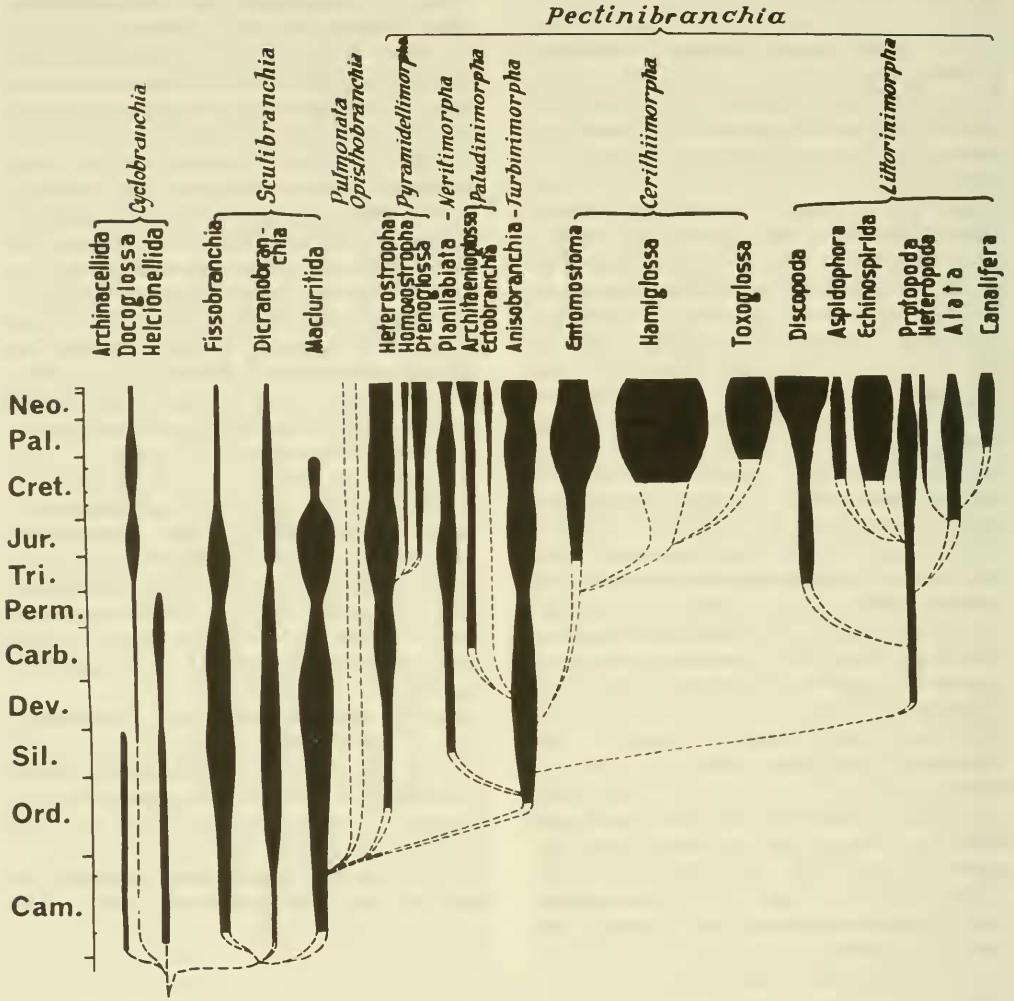
FIG. 6. Scheme of evolution and phylogeny of Gastropoda, particularly of prosobranch subclasses and orders (Opisthobranchia and Pulmonata are not considered in detail; Lepetellida are omitted). The width of the bands reflects the relative numbers of species in each phylogenetic branch at different geological times, from Cambrian to the Recent, calculated by the method of Schilder (1947).

SYSTEMATICS

Subclass CYCLOBRANCHIA Cuvier, 1817
    Order   Helcionellida[15] Knight, Batten & Yochelson, 1960 (as Helcionellacea)
        Superfamily   Helcionelloidea Wenz, 1938 (note 1)
               Coreospiridae Knight, 1947
               Helcionellidae Wenz, 1938
        Superfamily   Metoptomatoidea Wenz, 1938 (note 2)
               Metoptomatidae Wenz, 1938
    Order   Archinacellida Knight & Yochelson, 1958
               Archaeopragidae Horný, 1963
               Archinacellidae Knight, 1956
               (?) Hypseloconidae Knight, 1956
    Order   Docoglossa Troschel, 1866 (note 3)
        Superfamily   Patelloidea Rafinesque, 1815
               Damilinidae Horný, 1961
               Nacellidae Thiele, 1891
               Patellidae Rafinesque, 1815
        Superfamily   Tecturoidea Gray, 1847
               Tecturidae Gray, 1847 (Acmaeidae)
               Lottiidae Habe, 1944
               Pectinodontidae Thiele, 1893
        Superfamily   Lepetoidea Dall, 1869
               Propilidiidae fam. nov. (type-genus *Propilidium*
                  Forbes & Hanley, 1849)
               Lepetidae Dall, 1869
        Superfamily   Bathysciadioidea Dautzenberg & Fischer, 1900
               Bathysciadiidae Dautzenberg & Fischer, 1900
        (?) Superfamily   Bathypeltoidea Moskalev, 1971
               Bathypeltidae Moskalev, 1971
Subclass SCUTIBRANCHIA Cuvier, 1817
    Order   Dicranobranchia Gray, 1821 (note 4)
        Superfamily   Bellerophontoidea McCoy, 1851
               Sinuitidae Dall (in Zittel-Eastman), 1913
               Grandostomatidae Horný, 1962
               Temnodiscidae Horný, 1962
               Tropidodiscidae Knight, 1956
               Bucaniidae Ulrich & Scofield, 1897
               Salpingostomatidae Koken, 1925
               Carinaropsidae Ulrich & Scofield, 1897
               Pterothecidae Wenz, 1938
               Bellerophontidae McCoy, 1851
               Cymbulariidae Horný, 1963
               Knightitidae Knight, 1956
               Euphemitidae Knight, 1956
        Superfamily   Fissurelloidea Fleming, 1822 (note 4)
               Emarginulidae Gray, 1834
               Hemitomidae fam. nov. (type-genus *Hemitoma*
                  Swainson, 1840) [see footnote 14]
               Fissurellidae Fleming, 1822

[15]Some authors of recent works (e.g. Knight et al., 1960) have attempted to treat the name endings of orders (-ida) and suborders (-ina) uniformly. If this is desired, the names of those orders and suborders of our system that do not have these endings may be transformed into: Docoglossida, Dicranobranchida, Fissobranchida, Anisobranchida, Planilabiida, Architaenioglossida, Ectobranchida, Protopodida, Discopodida, Prionoglossina, Alida, Heteropodida, Canaliferida, Inoperculina, Involutina, Aspidophorida, Entomostomida, Hamiglossida, Rhiniglossina, Rhachiglossina, Nematoglossina, Toxoglossida, Heterostrophida, Entomotaeniina, Gymnoglossina, Ptenoglossida, and Homoeostrophida.

Order   Fissobranchia Stoliczka, 1868 (note 5)
          Superfamily   Rhaphistomatoidea Koken, 1896
                        Sinuopeidae Wenz, 1938
                        Rhaphistomatidae Koken, 1896
          Superfamily   Pleurotomarioidea Swainson, 1840
                        Eotomariidae Wenz, 1938
                        Lophospiridae Wenz, 1938
                        Luciellidae Knight, 1956
                        Phanerotrematidae Knight, 1956
                        Gosseletinidae Wenz, 1938
                        Portlockiellidae Batten, 1956
                        Catantostomatidae Wenz, 1938
                        Porcelliidae Broili, 1924
                        Rhaphischismatidae Knight, 1956
                        Phymatopleuridae Batten, 1956
                        Polytremariidae Wenz, 1938
                        Laubellidae Cox, 1960
                        Schizogoniidae Cox, 1960
                        Zygitidae Cox, 1960
                        Kittlidiscidae Cox, 1960
                        Temnotropidae Cox, 1960
                        Pleurotomariidae Swainson, 1840
                        Scissurellidae Gray, 1847
                        Trochotomidae Cox, 1960
          Superfamily   Murchisonioidea Koken, 1896 (note 6)
                        Murchisoniidae Koken, 1896
                        Plethospiridae Wenz, 1938
          Superfamily   Haliotoidea Rafinesque, 1815
                        Haliotidae Rafinesque, 1815
Order   Macluritida Cox & Knight, 1960
          Superfamily   Macluritoidea Fischer, 1885
                        Omphalocirridae Wenz, 1938
                        Macluritidae Fischer, 1885
                        Onychochilidae Koken, 1925
          Superfamily   Euomphaloidea de Koninck, 1881
                        Helicotomidae Wenz, 1938
                        Euomphalidae de Koninck, 1881
                        Omphalotrochidae Knight, 1945
          Superfamily   Pseudophoroidea S. A. Miller, 1889
                        Planitrochidae Knight, 1956
                        Euomphalopteridae Koken, 1896 (note 7)
                        Pseudophoridae S. A. Miller, 1889
          (?) Superfamily   Clisospiroidea S. A. Miller, 1889
                        Clisospiridae S. A. Miller, 1889 (note 7)
          Superfamily   Trochonematoidea Zittel, 1895
                        Trochonematidae Zittel, 1895 (note 7)

Subclass   PECTINIBRANCHIA Blainville, 1814
   Superorder   **Turbinimorpha** nov.
      Order   Anisobranchia v. Ihering, 1876
          Superfamily   Platyceratoidea Hall, 1859
                        Cyclonemidae S. A. Miller, 1889
                        Holopeidae Wenz, 1938
                        Platyceratidae Hall, 1859
          Superfamily   Microdomatoidea Wenz, 1938
                        Microdomatidae Wenz, 1938
                        Elasmonematidae Knight, 1956

(?) Superfamily   Codonocheiloidea S. A. Miller, 1889 (Craspedostoma-
                     tacea) (note 8)
                     Craspedostomatidae Wenz, 1938
                     Brochidiidae Yochelson, 1956
                     Crossostomatidae Cox, 1960
                     Codonocheilidae S. A. Miller, 1889

Superfamily   Anomphaloidea Wenz, 1938
                     Anomphalidae Wenz, 1938

Superfamily   Oriostomatoidea Wenz, 1938
                     Oriostomatidae Wenz, 1938
                     Tubinidae Knight, 1956

Superfamily   Paraturbinoidea Cossmann, 1916 (Palaeotrochacea)
                     (note 9)
                     Palaeotrochidae Knight, 1956
                     Paraturbinidae Cossmann, 1916

Superfamily   Turbinoidea Rafinesque, 1815 (note 10)
                     Turbinidae Rafinesque, 1815
                     Liotiidae Gray, 1850
                     Cyclostrematidae Fischer, 1885
                     Skeneidae Clarke, 1851
                     Phasianellidae Swainson, 1840

Superfamily   Trochoidea Rafinesque, 1815
                     Ataphridae Cossmann, 1918
                     Angariidae Thiele, 1921
                     Trochidae Rafinesque, 1815
                     Calliostomatidae Thiele, 1924
                     Umboniidae H. & A. Adams, 1858
                     Stomatellidae Gray, 1840

Superfamily   Eucycloidea Koken, 1896 (note 11)
                     Platyacridae Wenz, 1938
                     Cirridae Cossmann, 1916
                     Eucyclidae Koken, 1896 (Amberleyidae)
                     Notodelphinulidae Cox, 1960

Order   Lepetellida Moskalev, 1971 (note 12)

Superfamily   Lepetelloidea Dall, 1881
                     Lepetellidae Dall, 1881
                     Cocculinellidae Moskalev, 1971

Superfamily   Addissonioidea Dall, 1882
                     Addissoniidae Dall, 1882

Superorder   **Neritimorpha nov.**
Order   Planilabiata Stoliczka, 1868 (note 13)

(?) Superfamily   Cocculinoidea Dall, 1882
                     Cocculinidae Dall, 1882
                     Symmetrocapulidae Wenz, 1938

Superfamily   Titiscanioidea Bergh, 1890
                     Titiscaniidae Bergh, 1890

Superfamily   Hydrocenoidea Troschel, 1856
                     Hydrocenidae Troschel, 1856

Superfamily   Neritoidea Rafinesque, 1815 (note 13)
                     (?) Plagiothyridae Knight, 1956
                     Neritopsidae Gray, 1847
                     Neritidae Rafinesque, 1815
                     Septariidae fam. nov. (type-genus *Septaria* Férussac,
                       1807)
                     Phenacolepadidae Pilsbry, 1895
                     Payettiidae Dall, 1924
                     Dawsonellidae Wenz, 1938

Deianiridae Wenz, 1938
Helicinidae Férussac, 1822

Superorder   **Paludinimorpha** nov.
Order   Architaenioglossa Haller, 1894
Superfamily   Viviparoidea Gray, 1847
Viviparidae Gray, 1847
Pilidae Preston, 1915
(?) Pliopholygidae Taylor, 1966
Superfamily   Cyclophoroidea Gray, 1847 (note 14)
Dicristidae fam. nov. (type-genus *Dicrista* Thompson, 1969)
Amphicyclotidae Kobelt & Moellendorff, 1897
Neocyclotidae Kobelt & Moellendorff, 1897 (Poteriidae Thiele, 1929)
Crocidopomidae Thompson, 1967
Megalomastomatidae Kobelt, 1902
Cyclophoridae Gray, 1847
Ferussinidae Wenz, 1938
Craspedopomatidae Kobelt, 1902 (Maizaniidae Tielecke, 1940)
Spirostomatidae Tielecke, 1940
Pupinellidae Kobelt, 1902
Pupinidae H. & A. Adams, 1855
Hainesiidae Thiele, 1929
Cochlostomatidae Kobelt, 1902
Diplommatinidae Stoliczka, 1871
Order   Ectobranchia Fischer, 1884
Superfamily   Valvatoidea Gray, 1840
Valvatidae Gray, 1840
Superfamily   Tornoidea Sacco, 1896 (note 15)
Tornidae Sacco, 1896 (Adeorbidae; Vitrinellidae)

Superorder   **Littorinimorpha** nov.
Order   Protopoda Fischer, 1884
Superfamily   Turritelloidea Woodward, 1851
Turritellidae Woodward, 1851
Superfamily   Vermetoidea Rafinesque, 1815
Vermetidae Rafinesque, 1815
Tenagodidae Gill, 1871
Order   Discopoda Fischer, 1884 (note 16)
Suborder   Littorinina Pchelintsev, 1963 (as Littorinata) (note 17)
Superfamily   Littorinoidea Gray, 1840
Lacunidae Gray, 1857
Littorinidae Gray, 1840
Superfamily   Truncatelloidea Gray, 1840 (note 18)
Bithyniidae Gray, 1857
Pyrgulidae Brusina, 1881
Baicaliidae Fischer, 1885
Hydrobiidae Troschel, 1857
Lithoglyphidae Troschel, 1857
Emmericiidae Brusina, 1870
Fairbankiidae Thiele, 1928
(?) Tateidae Thiele, 1925
Stenothyridae Fischer, 1885
Truncatellidae Gray, 1840
Hyalidae fam. nov. (type-genus *Hyala* H. & A. Adams, 1852)

                           Littoridinidae Gray, 1857 (Pomatiopsidae Stimpson,
                              1865)
                           Benedictiidae Clessin, 1880
                           Fluminicolidae Clessin, 1880
                           Mexithaumidae Taylor, 1966
                           Lepyriidae Pilsbry & Olsson, 1951
      Superfamily   Pomatiasoidea Gray, 1852
                           Pomatiasidae Gray, 1852
                           Licinidae Pfeiffer, 1858 (Chondropomatidae)
                               (note 19)
      Superfamily   Aciculoidea Gray, 1850
                           Aciculidae Gray, 1850
      Superfamily   Assimineoidea Fischer, 1885
                           Assimineidae Fischer, 1885
      Superfamily   Barleeioidea Gray, 1857
                           Barleeidae Gray, 1857
      Superfamily   **Alvanioidea** nov.
                           Alvaniidae fam. nov. (type-genus *Alvania*
                               Risso, 1826) (note 20)
      Superfamily   Rissooidea Gray, 1847 (note 21)
                           Rissoidae Gray, 1847
                           Onobidae fam. nov. (type-genus *Onoba*
                               H. & A. Adams, 1852)
                           Anabathronidae Coan, 1964
                           Rissoinidae Stimpson, 1865
                           Merelinidae fam. nov. (type-genus *Merelina*
                               Iredale, 1915)
                           (?) Abyssochrysidae Tomlin, 1927 (note 22)
      Superfamily   Omalaxoidea Wenz, 1939
                           Omalaxidae Wenz, 1939
                           Circulidae Fretter & Graham, 1962
      Superfamily   Skeneopsoidea Iredale, 1915
                           Skeneopsidae Iredale, 1915
      Superfamily   Trachysmatoidea Thiele, 1925 (note 23)
                           Cingulopsidae Fretter & Patil, 1958
                           Eatoninidae fam. nov. (type-genus *Eatonina*
                               Thiele, 1912)
                           Trachysmatidae Thiele, 1925
  (?) Superfamily   Rastodentoidea Ponder, 1966 (note 24)
                           Rastodentidae Ponder, 1966
                           Lironobidae Ponder, 1967
      Superfamily   Caecoidea Gray, 1847
                           Ctiloceratidae Iredale & Laseron, 1957
                           Caecidae Gray, 1847
Suborder   **Rissoellina** nov. (note 16)
                           Rissoellidae Gray, 1850
Suborder   Prionoglossa G. O. Sars, 1878 (note 16)
                           Omalogyridae G. O. Sars, 1878
                           (?) Orbitestellidae Iredale, 1917 (Microdisculidae)
                               (note 25)
Order   Alata Lamarck, 1809
      Superfamily   Stromboidea Rafinesque, 1815
                           Eustomidae Cossmann, 1906
                           Aporrhaidae Gray, 1850
                           Harpagodidae Pchelintsev, 1963
                           Tibiidae nom. nov. (for Rostellariidae) (note 26)
                             [footnote 14]

                                        Terebellidae Korobkov, 1955
                                        Struthiolariidae Gabb, 1868
                                        Colombellinidae Fischer, 1884
                                        Strombidae Rafinesque, 1815
                  Superfamily   Seguenzioidea Verrill, 1884 (note 27)
                                        Seguenziidae Verrill, 1884
         Order   Heteropoda Lamarck, 1812 (note 28)
                  Superfamily   Atlantoidea Deshayes, 1830
                                        Atlantidae Deshayes, 1830
                  Superfamily   Pterotracheoidea Férussac, 1819
                                        Carinariidae Reeve, 1841
                                        Pterotracheidae Férussac, 1819
         Order   Canalifera Lamarck, 1809
                  Superfamily   Cymatioidea Iredale, 1913
                                        Cymatiidae Iredale, 1913
                                        Colubrariidae Cernohorsky, 1967
                                        Ranellidae Gray, 1854 (Bursidae Thiele, 1925)
                  Superfamily   Cassidoidea Latreille, 1825
                                        Cassididae Latreille, 1825
                                        Tonnidae Suter, 1913
                                        Ficidae Conrad, 1867
         Order   Echinospirida Fretter & Graham, 1962 (as Echinospiracea) (note 29)
              Suborder   Inoperculata Fischer, 1884
                  Superfamily   Vanicoroidea Gray, 1840
                                        Fossaridae Troschel, 1861
                                        Vanicoroidae Gray, 1840
                                        Hipponicidae Troschel, 1861
                  Superfamily   Calyptraeoidea Lamarck, 1809
                                        Trichotropidae Gray, 1850
                                        Lyocyclidae Thiele, 1925
                                        Capulidae Fleming, 1822
                                        Lamelliphoridae Korobkov, 1955
                                        Xenophoridae Philippi, 1856
                                        Calyptraeidae Lamarck, 1809
              Suborder   Involuta Fischer, 1884
                  Superfamily   Cypraeoidea Rafinesque, 1815
                                        Cypraeidae Rafinesque, 1815
                                        Ovulidae Fleming, 1828
                  Superfamily   Pedicularioidea Gray, 1853 (note 30)
                                        Triviidae Troschel, 1863
                                        Pediculariidae Gray, 1853
                  Superfamily   Lamellarioidea d'Orbigny, 1841
                                        Velutinidae Gray, 1842
                                        Lamellariidae d'Orbigny, 1841
                                        (?) Pseudosacculidae Hirase, 1928
         Order   Aspidophora Fischer, 1884
                                        Gyrodeidae Wenz, 1941
                                        Globulariidae Wenz, 1941
                                        Polinicidae Gray, 1847
                                        Sinidae Wenz, 1941
                                        Choristidae Verrill, 1882 (note 31)
                                        Naticidae Forbes, 1838
Superorder   Cerithiimorpha nov.
         Order   Entomostoma Blainville, 1824 (note 32)
                  Superfamily   Purpurinoidea Zittel, 1895
                                        Purpurinidae Zittel, 1895

Superfamily   Planaxoidea Gray, 1850
     Thiaridae Preston, 1915
     Planaxidae Gray, 1850
     (?) Brachytremidae Wenz, 1940
Superfamily   Melanopsoidea H. & A. Adams, 1854
     Melanopsidae H. & A. Adams, 1854
     Modulidae Fischer, 1885
Superfamily   Cerithioidea Férussac, 1819
     Procerithiidae Cossmann, 1905
     Eatoniellidae Ponder, 1965
     Litiopidae Gray, 1847
     Diastomidae Crosse & Fischer, 1893
     Bittiidae Cossmann, 1906
     Potamididae H. & A. Adams, 1854
     Pachychilidae Troschel, 1857 (Pleuroceridae
       Fischer, 1885)
     Paludomidae Gill, 1871
     Syrnolopsidae Bourguignat, 1890
     Cerithiidae Férussac, 1819
Superfamily   Cerithiopsoidea H. & A. Adams, 1854
     Cerithiopsidae H. & A. Adams, 1854
     Eumetulidae fam. nov. (type-genus *Eumetula*
       Thiele, 1912)
     Cerithiellidae nom. nov. (for Newtoniellinae
       Korobkov, 1960)
     Seilidae fam. nov. (type-genus *Seila* A. Adams, 1861)
Order   Hamiglossa Gray, 1853
   Suborder   Rhiniglossa G. O. Sars, 1878 (note 33)
     Triphoridae Gray, 1847
   Suborder   Rachiglossa Gray, 1853
Superfamily   Fasciolarioidea Gray, 1853
     Fusinidae Wrigley, 1927
     Fasciolariidae Gray, 1853
Superfamily   Buccinoidea Rafinesque, 1815
     Nassariidae Iredale, 1916
     Vexillidae Thiele, 1929
     Neptuneidae Troschel, 1869
     Melongenidae Gill, 1871
     Buccinulidae Powell, 1929
     (?) Pseudolividae Thiele, 1929 (note 34)
     Buccinidae Rafinesque, 1815
Superfamily   **Beringioidea** nov. (note 35)
     Anachidae fam. nov. (type-genus *Anachis*
       H. & A. Adams, 1853)
     Beringiidae fam. nov. (type-genus *Beringius*
       Dall, 1879)
Superfamily   Pyrenoidea Suter, 1913 (note 35)
     Pyrenidae Suter, 1913
Superfamily   Olivoidea Latreille, 1825 (note 36)
     Olivancillariidae fam. nov. (type-genus *Olivancillaria*
       d'Orbigny, 1841)
     Olividae Latreille, 1825
     Harpidae Brown, 1849
Superfamily   Marginelloidea Fleming, 1828 (note 36)
     Marginellidae Fleming, 1828
Superfamily   Volutoidea Rafinesque, 1815 (note 36)
     Volutidae Rafinesque, 1815

Superfamily Muricoidea Rafinesque, 1815 (note 37)
                  Muricidae Rafinesque, 1815
                  Vasidae H. & A. Adams, 1853
                  Coralliophilidae Hoyle, 1888 (Magilidae Thiele, 1929)
                  Thaididae Jousseaume, 1888
Suborder   **Nematoglossa** nov. (note 38)
                  Cancellariidae Gray, 1853
                  Admetidae Troschel, 1869
Order   Toxoglossa Gray, 1853
Superfamily Mitroidea Swainson, 1831
                  Mitridae Swainson, 1831
                  Cylindromitridae Cossmann, 1899
Superfamily Conoidea Rafinesque, 1815
                  (?) Speightiidae Powell, 1942
                  (?) Thatcheriidae Powell, 1942
                  Clavidae Powell, 1942
                  Cochlespiridae Powell, 1942
                  Turridae H. & A. Adams, 1855 (note 39)
                  Raphitomidae Bellardi, 1875
                  Conidae Rafinesque, 1815
                  Pervicaciidae Rudman, 1969
Superfamily Terebroidea Morch, 1852
                  Terebridae Mörch, 1852
Superorder   **Pyramidellimorpha** nov.
Order   Heterostropha Fischer, 1884 (note 40)
Suborder   Subulitina Pchelintsev, 1963 (as Subulitata)
                  Subulitidae Lindström, 1884
                  Meekospiridae Knight, 1956
Suborder   Entomotaeniata Cossmann, 1896
Superfamily Loxonematoidea Koken, 1889
                  Loxonematidae Koken, 1889
                  Palaeozygopleuridae Horný, 1955
                  Pseudozygopleuridae Knight, 1930
                  Zygopleuridae Wenz, 1938
                  Coelostylinidae Cossmann, 1909
                  Spirostylidae Cossmann, 1909
Superfamily Aclidoidea Thiele, 1925
                  Aclididae Thiele, 1925
Superfamily Pyramidelloidea d'Orbigny, 1840
                  Streptacididae Knight, 1931
                  Pyramidellidae d'Orbigny, 1840
                  Turbonillidae Locard, 1892 [footnote 14]
Superfamily Nerineoidea Zittel, 1873
                  Ceritellidae Wenz, 1938
                  Nerineidae Zittel, 1873
                  Nerinellidae Pchelintsev, 1960
                  Iteriidae Cossmann, 1896
Suborder   Gymnoglossa Gray, 1853 (note 41)
Superfamily Mathildoidea Dall, 1889
                  Mathildidae Dall, 1889
(?) Superfamily Trochaclidoidea Thiele, 1929
                  Trochaclididae Thiele, 1929
Superfamily Architectonicoidea Gray, 1840
                  Cyclostremellidae Moore, 1966
                  Architectonicidae Gray, 1840
                  Toriniidae Troschel, 1863

Order   Ptenoglossa Gray, 1853
          Superfamily   Epitonioidea Berry, 1910 (note 42)
                          Acirsidae Korobkov, 1955
                          Epitoniidae Berry, 1910
          Superfamily   Janthinoidea Lamarck, 1812
                          Janthinidae Lamarck, 1812
Order   Homoeostropha Fischer, 1885
          (?) Superfamily   Vellainelloidea Vasseur, 1880 (note 43)
                          Vellainellidae Vasseur, 1880
          Superfamily   Pseudomelanioidea Fischer, 1885
                          Pseudomelaniidae Fischer, 1885
                          Glauconiidae Pchelintsev, 1953
                          Trajanellidae Pchelintsev, 1953
          Superfamily   Eulimoidea H. & A. Adams, 1854 (Melanellacea)
                          Eulimidae H. & A. Adams, 1854
                          Stiliferidae Rosen, 1910
                          Asterophilidae Thiele, 1925 (note 44)
                          (?) Ctenosculidae Thiele, 1925
                          Paedophoropodidae Ivanov, 1937
                          Roseniidae Nierstrasz, 1913
                          Entoconchidae Fischer, 1883

NOTES

1. The category "superfamily" is used only when the families constituting an order or suborder can be assembled in more than one group. As regards the superfamily name endings (-oidea) see footnote 5.

2. Conchologically, the family Metoptomatidae is more similar to Helcionellidae than to Docoglossa; it therefore seems preferable to include it in the order Helcionellida.

3. The 3 generally accepted families of Docoglossa (Patellidae, Acmaeidae and Lepetidae) differ from each other so greatly as regards the structure of the mantle complex, the nervous system and the radula, that it appears more appropriate to consider them as 3 different superfamilies. The family Patellidae, in its commonly accepted scope, is divided into 2 independent families Nacellidae and Patellidae on the basis of anatomical data (Thiem, 1917a) and of its conchological peculiarities. In addition, we also include in this superfamily the family Damilinidae. Similarly the old family Acmaeidae Carpenter 1857, named by us Tecturidae in view of the independence of the genus *Tectura*, separates into 3 distinct families according to the development of their gills. The genus *Propilidium* Forbes & Hanley, 1849, is separated in an independent new family **Propilidiidae**, the characteristic feature of which is an apex which is markedly bent backwards and, according to

Forbes (Forbes & Hanley, 1850), the presence of 2 ctenidia. The genus *Propilidium* needs taxonomic revision as some forms conchologically different from the type species are also included in it. The family Bathysciadiidae is placed in the order Docoglossa within a separate superfamily following Moskalev's (1971) opinion. Another superfamily tentatively placed here consists of the family Bathypeltidae which is very similar to the Bathysciadiidae in radula and shell.

4. Because of structural diversity of shells in the families Sinuitidae and Bellerophontidae, as given by Knight et al. (1960), we return to Wenz's (1938) families, accepting them with some modifications in view of recent data. Sharply different genera were included in the family Cyrtolitidae by Knight and his co-workers. As was shown by Horný (1965), the genus *Cyrtolites* undoubtedly belongs to Monoplacophora, not because its species have numerous muscle scars but rather because of the location of its single pair of shell (i.e. columellar) muscle impressions, which are found in the periphery of the last whorl. Probably *Cloudia* and *Trigyra* are also related to this genus. On the other hand, other genera and especially *Cyrtodiscus*, which have no lateral keels and have an extension below the spiral, undoubtedly belong to Bellerophontoidea and must be included in the family Temnodiscidae (Horný, 1963b). Parallelism in shell structure of spiral Monoplacophora

and the lowest Gastropoda has been noted in another instance, viz. in the pair *Sinuitopsis* (Monoplacophora) - *Sinuites* (Gastropoda) (Rollins & Batten, 1968). The subfamily Bucanellinae (especially *Bucanella*) is probably near to *Sinuitopsis* and conse-quently belongs to Monoplacophora.

The family Fissurellidae commonly includes 3 clearly separate groups, accepted here as independent families: Emarginulidae with a cap-like shell preserving some traces of spirality and having an incision on the front part of the peristome or, rarely, a subapical opening; Hemitomidae fam. nov. with a cap-like shell devoid of a marked incision, but having a noticeable sulcus running from the apex to the front part of the peristome that is clearly visible when viewed from within the shell; and Fissurel-lidae with an incision in the form of an apical of subapical perforation on the cap-like shell, which has no trace of spirality.

5. Some families are excluded from the superfamily Pleurotomarioidea (= Pleurotomariacea) to form independent superfamilies. The families Sinuopeidae and Rhaphistomatidae, the characteristic fea-tures of which are a weakly developed incision and a tendency towards the for-mation of a depression, protuberance or sulcus on the periphery of the last whorl, are separated as a special superfamily Rhaphis-tomatoidea. The taxonomic position of this superfamily is not clear and we include it in the order Fissobranchia only provisionally. This superfamily seems to be artificial and probably some of its representatives are related to the order Macluritida. The family Haliotidae is separated as a special super-family Haliotoidea because its members have a distinctive ear-shaped shell and a number of incisions on the shell isolated from the shell margin. Phylogenetically this relatively young superfamily may be connected with the family Trochotomidae.

6. We consider Murchisonioidea to be a highly specialized group of Fissobranchia which has acquired some features common to Cerithioidea through convergence. The possibility of convergence of such kind occurring in the group is demonstrated by comparing Cerithioidea and Turritelloidea.

7. Euomphalopteridae and Trocho-nematidae, having no prominent fissure on the shell and only a canal, carina or depres-sion on the body whorl, are doubtlessly connected with the branch Macluritidae-

Euomphalidae, which has been separated as an independent order. Euomphalopteridae show a considerable conchological resembl-ance with Planitrochidae and Pseudo-phoridae (the genus *Crenilunula* is probably to be excluded from this family). The family Clisospiridae is only provisionally included in this order to form a special superfamily because this family may have developed from some pseudophorid ancestors.

8. The superfamily Codonocheiloidea (= Craspedostomatacea) is included in this group only provisionally in view of the conchological similarity of some of its genera with Turbinidae. The name has been changed according to the Law of Priority.

9. We use the name Paraturbinoidea instead of Palaeotrochacea according to the Law of Priority.

10. The families forming the tradi-tional superfamily Trochacea fall into 2 distinct groups, one of which has Trochidae as its central family while the other includes Turbinidae. These families are now grouped in 2 superfamilies, Turbinoidea and Tro-choidea, the former being considered more primitive than the latter in view of some similarity with Macluritida and of the neces-sity to include the highest Anisobranchia (*Calliostoma* in particular) in Trochoidea. The family Trochidae in its generally accepted scope is highly heterogeneous. It includes snails without pallial gonoducts (*Gibbula* and *Margarites*) and snails possessing one, though in a poorly developed form (*Cal-liostoma*) (see Fretter & Graham, 1962).

Taking into account the above con-siderations and the conchological peculiar-ities of different groups of genera we think it possible to raise the rank of the subfamily Calliostomatinae and consider it a separate family.

11. Recognizing the independence of the genera *Amberleya* and *Eucyclus*, we restore the oldest name for the family (and superfamily) i.e. Eucyclidae Koken, 1896, for Amberleyidae Wenz, 1938.

12. The arrangement of families of the order Lepetellida is given after Moskalev (1971). The superfamily Bathypeltoidea, however, has been tentatively placed in the cyclobranch order Docoglossa.

13. The superfamily Cocculinoidea (with the family Symmetrocapulidae) is included in the order Planilabiata after Moskalev (1971). The old superfamily Neritacea must be divided into 3 inde-

pendent ones: Titiscanioidea, Hydro-
cenoidea (both with a monaulic, but still
very different female gonoduct), and Neri-
toidea (with a di- or triaulic female gono-
duct). In the latter superfamily we set up a
new family **Septariidae**, having a triaulic
female gonoduct instead of the diaulic ar-
rangement found in the Neritidae.

14. Anatomical differences between
the groups of Cyclophoridae, s.l., are very
great (Tielecke, 1940; Thompson, 1969) and
comparable to the differences existing be-
tween Pilidae and Viviparidae. For this
reason we treat the subfamilies accepted by
these authors as separate families. We are
also making some nomenclatorial changes:
Maizaniidae Tielecke, 1940 = Crasp-
edopomatidae Kobelt, 1902, and Poteriidae
Thiele, 1929 = Neocyclotidae Kobelt &
Moellendorff, 1897. Furthermore we add
the family **Dicristid**ae fam. nov., in members
of which renal, bursal and pallial parts of the
female gonoduct open independently into
the mantle cavity (see footnote 16). The
group Dendropupinae Wenz, 1938, judging
by the shells of *Anthracopupa* and *Maturi-
pupa*, belongs to the Carychioidea, subclass
Pulmonata.

15. The family Tornidae (= Adeor-
bidae Monterosato, 1884; Vitrinellidae Bush,
1897) is included in the order Ectobranchia
only provisionally, on the basis of ana-
tomical data on *Tornus* (Woodward, 1899)
which are somewhat inadequate.

16. The main group of the order
Discopoda consists of families having a
taenioglossate radula and either a single or a
double pallial gonoduct. In the latter group
these 2 gonoducts run distally from the end
of the renal gonoduct, one being the usual
glandular tube and the other either a ciliated
groove or another tube running parallel to
the first, and opening by a special orifice.[16]
Gastropods with a complex hermaphroditic
system go back to forms with a double
pallial gonoduct. They form 2 independent
groups with different structures of the repro-

ductive system and of the radula. We there-
fore isolate these 2 groups as special
suborders **Rissoellina** (new) and Priono-
glossa, leaving the bulk of the other families
of the order Discopoda in the suborder
Littorinina.

17. Due to the vast diversity in struc-
ture of the reproductive systems of the
gastropods formerly classified in the super-
families Littorinacea and Rissoacea we
divide the suborder into a considerably
greater number (13) of superfamilies.

Among the members of the 2 old
superfamilies one may distinguish 3 groups:
(1) families whose members have a pallial
gonoduct with equally thickened glandular
walls (Aciculidae, Assimineidae and Barle-
eidae); (2) families with a pallial gonoduct
with a longitudinal ventral ciliary groove
separated, to a greater or smaller degree,
from the glandular part (Littorinacea, Ris-
soidae and Hydrobiidae, in their former
extent); and (3) families with a double
pallial portion of the female reproductive
system; in these, the glandular part has the
same structure as in the 1st group; besides
they have an independent ciliary groove
(Skeneopsidae) or a separate duct (Cingulop-
sidae) running parallel to this part. Ana-
tomical data (Rao, 1928; Krull, 1935;
Fretter & Patil, 1958; Fretter & Graham,
1962; Jackiewicz, 1967) show that the
families forming the 1st group are rather
remote taxonomically and should be
separated into 3 special superfamilies:
Aciculoidea, Assimineoidea and Barle-
eioidea. The families of the 3rd group are
provisionally placed in 2 superfamilies
Skeneopsoidea and Trachysmatoidea (see
also note 23) on conchological grounds.
However, the taxonomic position of the
genera of this group needs more detailed
studies. The families of the 2nd group,
which is the largest, may be divided into 5
superfamilies on the basis of the structure of
the genital system: (1) the forms with a
virtually unclosed pallial gonoduct (such as

[16]For a more precise homologization, the constituents of the reproductive system may be defined as having
the following limits: the visceral gonoduct runs from the gonad to the gonopericardial duct, the renal
gonoduct from the gonopericardial duct to the "bursal" duct; the pallial gonoduct runs distad from the
"bursal" duct (or from the nephropore, where it is preserved transformed). Though the bursa (a name
here used to designate the sac opening into the base of the pallial gonoduct in Discopoda) is of pallial
origin, it cannot be considered a part of the pallial gonoduct; it is a rather special structure that appeared
independently from the closing of the mantle folds. Probably it is a primary sperm-receiving reservoir,
originally opening into the mantle cavity near the urogenital papilla (as is the case in Cocculinidae). The
name "bursa" ("bursa copulatrix") is often applied to other sacs, such as the distal sac of the pallial
gonoduct (which we call the spermatheca) or (in Entomostoma) to the sac opening in the middle of the
pallial gonoduct. It is clear that neither organ has anything to do with the bursa of Discopoda.

Pomatiasidae) are included in a special super-family Pomatiasoidea; (2) the forms having one gland in the pallial gonoduct and one gland in the renal gonoduct (Rissoidae, Onobiidae, etc.) are included in the super-family Rissooidea (see also notes 21, 22); (3) the group whose members have one gland in the pallial gonoduct and no gland in the renal gonoduct (Alvaniidae; see note 20) is separated as a new superfamily Alvanioidea; (4) families with 2 glands in the pallial gonoduct (Pyrgulidae, Baicaliidae and Hydrobiidae, s.l.) are included in the super-family Truncatelloidea (see also note 18). (5) the old superfamily "Littorinacea" is the last superfamily of this group. To these 10 superfamilies we add another 3, as the structure of their shells and radulae prevents their inclusion in any of the above men-tioned superfamilies in the suborder Lit-torinina. These are: the Caecoidea, the char-acteristic features of which are a closed pallial gonoduct and the presence of a penis, which has prevented us from including them in Cerithiacea; the Omalaxoidea, with the two families Omalaxidae and Circulidae (the characteristics of the latter family are found in Fretter (1956:381)), and, tentatively, the Rastodentoidea, with Rastodentidae (see also note 24) and Lironobidae.

18. The families included in the super-family Truncatelloidea previously belonged either to Hydrobiidae, s.l., and Rissoidae or were considered independent (e.g. Baicali-idae). The families whose members have been studied anatomically are characterized by their reproductive systems as follows:

Bithyniidae. The bursa is present, but there is no seminal receptacle. The renal gonoduct is greatly thickened and has the shape of a long irregularly coiled tube. The ventral groove is separated by the folds of the glandular part, formed by 2 successive glands. The prostate is band-shaped and consists of diverticula opening into the vas deferens. The copulatory apparatus has 1 or 2 accessory glands (anatomical data of Bregenzer, 1916; Seshaiya, 1930; Krull, 1935; Lilly, 1953).

Pyrgulidae. The female reproductive system is somewhat similar to that of the previous family. But instead of a true seminal receptacle in the female renal gono-duct there is a pouch which does not differ histologically from the adjoining parts of the renal gonoduct. The prostate is kidney-shaped and consists of a great number of diverticula. The copulatory apparatus has no accessory glands (anatomical data of Kozhov, 1951; Radoman, 1955).

Baicaliidae. The female reproductive system has the same structure as in Pyrguli-dae, but the renal gonoduct has several caeca serving as the seminal receptacle (anatomical data of Kozhov, 1951).

Hydrobiidae. The female reproductive system also has the same general structure, but the renal gonoduct is short, thin and almost uncoiled; there is a true seminal receptacle, which is not connected, however, with the bursa through a reservoir. The male reproductive system resembles that of Pyrgulidae (anatomical data of Quick, 1920; Robson, 1922; Krull, 1935; Fretter & Graham, 1962).

Lithoglyphidae. The glandular part of the female pallial gonoduct consists of 2 glands, and is separated from the ventral groove by several folds. There are 1-2 se-minal receptacles. The renal gonoduct is greatly thickened and has the shape of a long irregularly bent tube. The male reproductive system is the same as in Pyrgulidae (ana-tomical data of Siebold, 1904; Krull, 1935; Krause, 1949; Radoman, 1955, 1963, 1965, 1966a, 1966b, 1967b; Bole, 1961, 1967).

Emmericiidae. The pallial gonoduct has 2 (?) glands and a ventral canal, separ-ated by a fold and considerably dilated in the distal part. The bursa and the seminal receptacle are present. The renal gonoduct has the shape of a long, thick and coiled tube. The prostate is kidney-shaped and has a great number of diverticula. The copu-latory apparatus has 2 accessory glands (anatomical data of Radoman, 1967a).

Truncatellidae. The pallial gonoduct of the female has 2 consecutive glands and a ventral groove, separated by a fold. The bursa and the seminal receptacle are present. Their ducts are connected to each other by a short duct; the bursa duct is also connected to the left kidney. The male reproductive system is the same as in Pyrgulidae (ana-tomical data of Vayssière, 1885; Fretter & Graham, 1962).

Hyalidae fam. nov. The glandular part of the female pallial gonoduct consists of 2 glands placed one after the other; the ventral groove is separated by a fold. The bursa is present; no seminal receptacle, but a sperma-theca is present. The female genital pore is located midway on the pallial gonoduct. The shell is small, slender and smooth with a

stained periostracum (anatomical data of Johansson, 1950, on *Hyala*).

Littoridinidae (= Pomatiopsidae). Bursa and seminal receptacle are present. The pallial gonoduct of the female has 2 glands located one after the other. The ventral groove is set apart from the glandular part either completely or only in the distal half and closes to form a duct opening into a special orifice. The male reproductive system is as in Pyrgulidae (anatomical data of Robson, 1920, 1921; Li Fu-Ching, 1934; Krull, 1935; Itagaki, 1955; Van der Schalie & Dundee, 1956; Roth & Wagner, 1957; Patil, 1958; Roth, 1960; Davis, 1967).

Benedictiidae. Bursa and seminal receptacle are present; they adjoin each other closely, sharing a small area of wall which usually has a perforation or a connecting canal. The renal gonoduct is comparatively short and thin. The pallial gonoduct of the female has 2 glands one after the other. The ventral groove is set apart only by folds. The male reproductive system is as in Pyrgulidae (anatomical data of Kozhov, 1945, 1950).

The remaining families are included here on the basis of the structure of their shells and radulae. In the family Fluminicolidae are included, besides the type genus, a number of *Lithoglyphus*-like East Asiatic forms (*Lithoglyphopsis, Jullienia, Fenouilia, Lacunopsis* and *Wykoffia*); in the family Mexithaumidae, besides the type genus, *Potamolithus, Potamolithoides* and *Lithococcus.* The latter 2 families need careful anatomical and taxonomic study.

19. We use the name Licinidae and not Chondropomatidae according to the Law of Priority.

20. The new family **Alvaniidae** may be defined as follows: the shell is oval-conical, small, solid with reticular or, rarely, with only spiral sculpture and an oval aperture pointed upwards. The operculum is corneous, paucispiral, without any processes. The radular formula is 3.1.3. The rachidian and lateral teeth of the radula have large rounded cusps, the marginal teeth small cusps. No gland is present in the renal gonoduct of the female, but there is a widening. There are 1-2 seminal receptacles and a bursa; the ventral groove is set apart from the glandular part of the pallial gonoduct by several longitudinal folds. There is only 1 gland here. The prostate is cylindrical; the vas deferens is connected with the mantle cavity near the proximal end of the prostate (anatomical data of Johansson, 1956b).

21. The new family **Onobidae** differs from Rissoidae by the presence of a prostate and a connection between the vas deferens and anterior (not posterior as in Rissoidae) part of the mantle cavity. The shell is oval, oval-conical or top-shaped, either with dominant spiral sculpture or almost smooth, with a rounded or rounded-oval aperture that does not point upwards. The operculum is corneous, paucispiral. The radula is as in Rissoidae and Alvaniidae (anatomical data of Johansson, 1948; Fretter & Graham, 1962). To the Rissooidea we also add the families Anabathronidae (anatomical data of Ponder, 1967, 1968), Rissoinidae, whose anatomy was presented by Kosuge (1965) and **Merelinidae** fam. nov., the members of which differ from Rissoinidae by the presence of a prostate and by the subterminal position of the female aperture, which in Rissoinidae is located in the depth of the mantle cavity far behind the anus. Data on the anatomy of members of the Merelinidae are found in Ponder (1967, 1968). We also include in this family "*Rissoina*" *chathamensis* (Hutt.) because it has a prostate.

22. Because of the presence of a cephalic copulatory apparatus we exclude the family Abyssochrysidae from Cerithiacea and add it to Discopoda, where we provisionally include it in Rissooidea, guided by the characters of its shell.

23. We include in the superfamily Trachysmatoidea in addition to the family Trachysmatidae which has not been studied anatomically: Cingulopsidae, which are conchologically similar to Trachysmatidae, and **Eatoninidae** fam. nov., the members of which are similar to *Cingulopsis* in the structure of the reproductive system but differ by the absence a second pallial duct connecting the distal end of the renal gonoduct with the mantle cavity. Moreover, Eatoninidae differ from Cingulopsidae by the conical shell.

24. The family Rastodentidae (= Rastodenidae) is included provisionally in the Littorinina. Taxonomically, if the shell and radula are the guiding factors, it can be considered close to Lironobidae. It is to be stressed that the radula structure (Ponder, 1966, 1967) sets these 2 families apart from other Littorinina.

25. The family Orbitestellidae (= Microdisculidae) is provisionally included in this suborder following Thiele (1929).

26. The new name **Tibiidae** is used by us instead of Rostellariidae in view of the priority of the name *Tibia* Bolten in Röding, 1798 over *Rostellaria* Lamarck, 1799.

27. Some scientists (Thiele, 1929) place *Seguenzia* in Trochacea; others (Taylor & Sohl, 1962) have provisionally placed Seguenziidae in Cerithiacea. From the structure of the shell and the peculiar radula of a single representative of this family, which is very inadequately studied anatomically, we include it in the order Alata as a special superfamily.

28. The order Heteropoda is divided into 2 superfamilies. In one of them (Atlantoidea) we include forms with a developed shell and operculum; in the other (Pterotracheoidea), the forms with rudimentary shells.

29. The order Echinospirida is divided into 2 suborders, Inoperculata and Involuta, on the basis of their special structure, ecology and evolution. The characteristic feature of the suborder Inoperculata, which developed from a semi-filtrating mode of nutrition to ectoparasitism, is the transition from a spirally coiled shell to a cap-like external shell, often with a septum inside it. The suborder Involuta, which progressed to predation, is characterized by the formation of an involute or ear-shaped shell and by the mantle overgrowing the shell to the point even of complete enclosure of the shell.

30. We separate the superfamily P e d i c u l a r i oidea (= Triviacea) following Schilder (1966), leaving the superfamily Lamellarioidea including only the families Lamellariidae, Velutinidae and, provisionally, Pseudosacculidae.

31. We provisionally include the family Choristidae in the order Aspidophora on the basis of shell characters and the shape of the radular teeth.

32. The order Entomostoma comprises groups that have usually been placed in Cerithiacea, as well as the Purpurinidae, transferred from the Littorinacea, as they are conchologically more similar to the lower Entomostoma. The old superfamily Cerithiacea remains highly heterogeneous even after we removed from it a number of families and assigned them to other orders. Its heterogeneous character becomes particularly evident when available anatomical data (Moore, 1898, 1899a, 1899b; Seshaiya, 1934; Johansson, 1947, 1953, 1956a; Morrison, 1954; Binder, 1959; Dazo, 1965) are analyzed. We therefore divide this superfamily into 4 smaller superfamilies. Into one of them, Planaxoidea, we place forms devoid of a true pallial gonoduct, having a ciliary mantle groove, and, besides, a special chamber for the incubation of eggs which is not of mantle origin. Two other superfamilies, Melanopsoidea and Cerithioidea, may be characterized as having a well developed but longitudinally unclosed pallial gonoduct. In Melanopsoidea, which comprise Melanopsidae and Modulidae, it is open only in females, which have a special ovipositor. In Cerithioidea it is not closed, or only partially closed in both sexes. In this superfamily we also include, next to Cerithiidae: Potamididae, Bittiidae, Pachychilidae (= Pleuroceridae), Paludomidae—which we consider an independent family in view of the marked differences between it and Pachychilidae in the structure of the female and male reproductive system—and Eatoniellidae, on the basis of Ponder's (1965, 1968) anatomical findings. Also included are families for which anatomical data are either very scanty or non-existent.

The family Cerithiopsidae cannot be included in any of the above 3 superfamilies because sperm transmission is carried out by spermatozeugmata, as in Ptenoglossa. We divide it into 4 families because of the vast diversity of its members, which we place in a 4th superfamily Cerithiopsoidea.

The family Cerithiopsidae, s.s., may be characterized by the presence of a multispiral protoconch, which differs markedly from the definitive shell by the steepness of coiling; a spirally nodular sculpture of the definitive whorls; a very weakly developed siphonal process with a wide canal; and characteristic radular teeth similar to those in Cerithioidea.

The family **Eumetulidae** fam. nov. has the following characteristic features: a paucispiral protoconch, spirally nodular sculpture of the definitive whorls and a wide apertural canal without a siphonal process. The radular teeth are wide and supplied with a great number of small cusps.

The characteristic features of the family **Cerithiellidae** nom. nov. (for Newtoniellinae Korobkov, 1960) are the following: a paucispiral protoconch; a spirally nodular structure of the definitive whorls;

the presence of a basal keel; a well developed oblique siphonal process and a radula furnished with hook-like lateral and marginal teeth and an almost square rachidian tooth bearing 1-5 cusps.

The family **Seilidae** fam. nov. is characterized by a paucispiral protoconch; smooth spiral sculpture of the definitive whorls; absence of the siphonal process accompanied by a wide apertural canal; and by a radula with a tricuspid rectangular rachidian tooth, several small tetragonal unicuspid lateral teeth and a very small hook-ended marginal tooth.

We expect that some of the families here included in the Entomostoma will be placed in other orders after careful anatomical studies.

33. Risbec (1955) showed anatomically that Triphoridae are closer to Stenoglossa than to Cerithiacea. This is also confirmed by the structure of the radula, which cannot be reduced from the taenioglossate type. Nevertheless, they cannot be included in the main group of Stenoglossa (i.e. Rachiglossa). We therefore separate it as a special suborder Rhiniglossa.

34. The subfamily Pseudolivinae, being rather far from other Olividae as to shell characters and differing greatly from them by their radula, is elevated to family rank, the more so as the remaining Olividae are also highly heterogeneous and should be divided into at least 2 families. On the basis of shell structure and radula we assign the family Pseudolividae to the superfamily Buccinoidea.

35. Columbellidae, s.l., are highly heterogeneous. They cannot be included in Buccinoidea. In our classification they are divided into 2 superfamilies: Beringioidea and Pyrenoidea. In Beringioidea, as seen by the anatomy of *Anachis*, males have no prostate and females have a renal albumen gland, the sperm receiving sac being situated in the distal part of the pallial gonoduct. In Pyrenoidea, as seen from the anatomy of *Mitrella lunata* (Say)[17] and *Pterygia= Columbella*, males have a prostate and females have neither albumen gland nor sperm receiving sac, the functions of which are performed by the pericardium (Marcus & Marcus, 1962). In the first of these superfamilies we distinguish 2 families. The new family **Beringiidae** may be described as

follows: the shell is dilated and spindle-like; it has convex whorls, a wide, short siphonal process, which is slightly bent backwards, a relatively large embryonic shell and a well developed periostracum. Spiral sculpture clearly predominates over axial sculpture. The corneous operculum has a terminal nucleus and no ornamentation. The radula exhibits an edentate rachidian lamina and lateral laminae, which in general outline are similar to those in Pyrenidae. This young family, which may have appeared as late as the Miocene, inhabits cold and temperate waters in the Northern Hemisphere and is represented for the time being by 2 genera only, *Beringius* and *Liomesus*. **Anachidae**, the second new family of the Beringioidea, shows the following characteristics: the shell is spindle-shaped, either smooth or with axial ribs and spiral sculpture that is more prominent at the basal portion of the last whorl; the siphonal process is short, the palatal margin of the aperture is denticulate within; no prostate; the renal gonoduct of the male has a widening ("seminal vesicle"), the female has a renal albumen gland and a complicated spermatheca, opening into the distal portion of the pallial gonoduct; no gonopericardial duct in adults.

36. The studies by Olsson (1956) and Marcus & Marcus (1959) clearly show that Olividae, s.l., appeared and developed independently of Volutidae, with which they are often associated taxonomically, and parallel to Buccinoidea and Muricoidea. Following Olsson, we set apart Olividae, creating for them a special superfamily. Marginellidae are also separated as a special superfamily as they have an extremely peculiar radula (i.e., one with a single pluricuspid lamina) which is not derived from the radulae of Olividae or Volutidae. In the superfamily Olivoidea, we include next to Olividae and Harpidae, which are probably connected with Olividae, the new family **Olivancillariidae**, whose members differ from true Olividae by a peak-shaped shell with a short spire, by the presence of some additional cusps on the rachidian tooth of the radula and by a peculiar female reproductive system, in which the albumen gland, 2 sperm-receiving sacs and the gland of the pallial gonoduct have a common orifice opening into the posterior portion of the mantle cavity.

37. We include 4 families in the super-

[17]But the Northwest Pacific *Mitrella burchardi* (Dkr.) doubtlessly belongs to the family Anachidae (personal anatomical investigation).

family Muricoidea, among which Vasidae, which are usually placed among Volutacea, on account of a very peculiar structure of the shell and radula, and Thaididae, which, following Pchelintsev et al. (1960), we also consider an independent family, with Thaidinae (= Purpurinae Lamarck, 1809) and Rapaninae as subfamilies.

38. Cancellariidae and Admetidae are placed in a new suborder that we name **Nematoglossa** on the basis of: (1) distinct external and internal morphology; (2) more important yet, a most peculiar radula, differing greatly from that found in other representatives of the order Hamiglossa, and (3) a very characteristic direction in their evolution, showing a marked tendency towards complete reduction of the radula. Cancellariidae, having a strong shell with plicae on the columellar margin of the aperture, and possessing a radula, are phylogenetically older than Admetidae, that have no radula and a very thin shell, and should be considered a special family.

39. Powell (1942, 1964), who specialized in the taxonomy of the Turridae, s.l., attaches great importance to the shell and believes that the differences in the structure of the radula reflect different stages in the transition to the classical toxoglossate type, in which the rachidian and lateral teeth disappear completely. We doubt the validity of this approach on the one hand because in some forms the radula shows a specialized tendency towards stronger lateral (*Drillia*) or rachidian (*Leucosyrinx* and *Ptychosyrinx*) teeth. On the other hand, the features on which Powell has based his division of the Turridae into subfamilies may appear independently (Amitrov, 1968). We therefore divide the Turridae into 4 independent families: Clavidae, having laminar pluricuspid laterals and a small rachidian tooth (here belong the genus *Clavus* and a large part of the subfamily Clavinae as Powell understood it); Cochlespiridae, in which the lateral teeth have disappeared, whereas the rachidian exists in a highly developed form (here belong part of Powell's Cochlespirinae, probably the extinct genus *Cochlespira* and also the genera *Ptychosyrinx* and *Tur-*

ridrupa); Turridae, s.s., without lateral teeth, the rachidian being either rudimentary or completely absent, though the basal membrane of the radula is preserved; and Raphitomidae, having a radula of the classical toxoglossate type lacking lateral and rachidian teeth and also a basal membrane.

40. In the order Heterostropha we distinguish 3 suborders: Subulitina, Entomotaeniata and Gymnoglossa, characterized by an independent direction of evolution. In Entomotaeniata we place families with a turriform shell, often with a plicate columella, and with sloping excavations on the basal and palatal margins of the aperture. The characteristic features of its Recent representatives, in addition to those mentioned above, are a separated anterior part of the foot ("mentum"), a reduced radula, a more complex reproductive system (due mainly to hermaphroditism) and a considerably concentrated nervous system. The most specialized members of this group, Pyramidelloidea, have even been recently included in Opisthobranchia or Euthyneura. We are inclined to think, however, that all the features characteristic of Pyramidellidae discussed in support of this view (see Fretter & Graham, 1962) may have developed independently because of their small size and their peculiar mode of life or, in some cases, have been inherited from some ancestor common to them and to the lowest Opisthobranchia and Pulmonata. The suborder Gymnoglossa,[18] whose members retain their radula (which shows a gradually decreasing number of teeth), have comparatively simple alimentary and reproductive systems. The Subulitacea fail to fit in either of the other 2 suborders as it combines features of the Entomotaeniata and of the orders Ptenoglossa and Homoeostropha. For this reason we set it apart in a special suborder Subulitina. Heterostrophy occurs in the superfamilies Pyramidelloidea, Nerineoidea, and in the gymnoglossate Mathildoidea and Architectonicoidea. It does not occur in Aclididae and is not likely to be found in other groups. We may assume that in this order heterostrophy was inherited from some very remote ancestors that were also

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[18]The term Gymnoglossa (naked tongue) was proposed by Gray (1853) for forms "with teeth and lingual membrane rudimentary or none." The taxon Gymnoglossa, however, included a number of heterogeneous groups, among which are the Architectonicidae. After the removal of most of these groups (e.g. Pyramidellidae, Tylodinidae, Cerithiopsidae, Cancellariidae, etc.) the name may now be retained for Architectonicidae, even though they do have a radula.

common to Opisthobranchia and Pulmonata, and lost many times within the order (see also Minichev & Starobogatov, 1971).

41. The families which we include in the suborder · Gymnoglossa are distributed among 3 superfamilies: one of them contains the single family Mathildidae, which still retains a very strong rachidian tooth and has a characteristic shell, resembling that of Entomotaeniata; another includes Architectonicidae and similar forms, which have either markedly reduced or no rachidians, and in addition a top-shaped or planispiral shell. The Architectonicidae and Toriniidae, though, are rather heterogeneous as to their radulae and may have to be divided into a number of smaller families. The 3rd super- family contains the Trochaclididae. This family certainly cannot be classified in the order Discopoda, where it would be included if we left it in the Rissoacea, following Thiele (1929); it may be placed either in Gymnoglossa or perhaps Ptenoglossa, stand- ing somewhat apart. The problem can be solved only by careful anatomical studies of *Trochaclis* and of Architectonicidae.

42. Sharp distinctions in the form and degree of shell scalarity, in the shape of the shell and also in the form of the radular teeth allow us to distinguish 2 families in the superfamily Epitonioidea: Epitoniidae and Acirsidae. Both appeared at the juncture of the Triassic and Jurassic and evolved in parallel. Janthinidae may have developed from ancestors common with Epitoniidae.

43. This extinct group is excluded from Trochacea (now in the superorder Turbinimorpha) because of its shell shape and is provisionally placed in the order Homoeostropha as a separate superfamily.

44. Asterophilidae are included in this s u p erfamily following Gruzov (1965). Ctenosculidae may also belong here, though available information on their anatomy does not constitute adequate proof.

ACKNOWLEDGMENTS

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АБСТРАКТ

СИСТЕМАТИКА ПЕРЕДНЕЖАБЕРНЫХ МОЛЛЮСКОВ

А.Н. ГОЛИКОВ И Я.И. СТАРОБОГАТОВ

В пределах класса брюхоногих моллюсков авторы намечают 5 основных направлений эволюции и как следствие этого 5 главнейших таксономических подразделений, различающихся важнейшими особенностями строения. Три из них, как правило, объединяются в подкласс **Prosobranchia**. Однако своеобразие морфологической структуры и направления эволюции в каждом из свое трех подразделений рассматриваются как равноценные таковым у этих остальных подклассов брюхоногих т.е. у **Opisthobranchia** и **Pulmonata**. Вследствие этого переднежаберные моллюски разделяются на 3 самостоятельных подкласса **Cyclobranchia**, **Scutibranchia** и **Pectinibranchia**.

Cyclobranchia (т.е. **Docoglossa** в прежнем понимании и некоторые палеозойские группы) представляют собой особую линию эволюции, характеризующуюся примитивной первично-симметричной раковиной, лишенной вырезки или желобка, архаичным, не встречающимся у других брюхоногих типом строения и движения радулы, а также строением желудка, половой и нервной систем, которые у **Cyclobranchia** сходны с таковыми **Scutibranchia**. Кроме того асимметрия мантийного комплекса, развившаяся независимо у представителей этой группы, специализация радулы, развитие артериального бульбуса и наличие мантийных нервных стволов поддерживает мнение, что эта группа имеет свое направление эволюции. Исходя из этих доводов, **Cyclobranchia** выделяются в особый подкласс, включающий отряды **Helcionellida**, **Archinacellida** (ранее относимый к **Monoplacophora**) и **Docoglossa**. Эволюционный процесс в этой группе был морфологически выражен уменьшением размеров и степени развития скульптуры раковины, олигомеризацией радулы и редукцией специализированных органов дыхания в ходе эволюции.

Остальные брюхоногие происходят от древней группы моллюсков, возникших от примитивных **Cyclobranchia** в кембрийский период; эти моллюски имели симметричный мантийный комплекс и медиально расположенную вырезку (или желобообразный выступ).

Сохранение симметрии мантийного комплекса в ходе эволюции, параллельное развитие вырезки, хорошо выраженный эпиподий и отсутствие достаточно развитых ганглиев центральной нервной системы при заметном развитии симметричных бранхиальных ганглиев позволяют выделять отряды **Dicranobranchia**, **Fissobranchia** и **Macluritida** в особый подкласс **Scutibranchia**. Эволюция в пределах **Scutibranchia** выявляет тенденцию в ходе филогенеза к уменьшению размеров и степени закрученности раковины, к обособлению и смещению вырезки от края устья, к уменьшению роли спиральной скульптуры, при возрастании роли осевой и к увеличению размеров правой почки в связи с выполнением ею двоякой функции: выделительной и половой.

Подкласс **Pectinibranchia**, включающий **Monotocardia** (**Mesogastropoda** и **Neogastropoda**), а также **Trochacea** и **Neritacea** из **Diotocardia** (=**Archaeogastropoda**) прежних классификаций, филогенетически самый молодой и наиболее разнообразный по морфологическому строению, возник в недрах **Scutibranchia** (скорее всего от **Macluritida** или общих с ним предков).

В пределах **Pectinibranchia** выделяются 18 отрядов, характеризующихся общим планом строения и следующих основной эволюционной тенденции всего подкласса, но в то же время каждый из них представляет свою особую линию развития и имеет свои особенности строения раковины, ноги, пищеварительной системы, жабры, центральной нервной системы, половой системы и экологии. Из этих 18 отрядов наиболее ранней дивергенции подверглись две группы: одна, рассматриваемая здесь как надотряд **Pyramidellimorpha** и другая, представленная **Anisobranchia** (=надотряд

Turbinimorpha) вместе со связанными с ней филогенетически отрядами, объединенными здесь в новые надотряды **Neritimorpha, Paludinimorpha, Littorinimorpha** и **Cerithiimorpha.**

Эволюционное развитие подкласса, часто проявляющееся параллельно в разных отрядах и надотрядах, морфологически выражается в уменьшении степени развития скульптуры, (особенно спиральной), образовании сифонального выроста, исчезновении эпиподия, редукции челюсти, олигомеризации радулы, осуществляющейся в разных группах различными путями, усилении асимметрии мантийного комплекса, образовании гребенчатых ктенидия и осфрадия, превращении правой почки в ренальный гонодукт и концентрации и интеграции центральной нервной системы. Эволюция в пределах разных подразделений **Pectibranchia** шла параллельными путями от исходной микрофагии, сестонофагии и фитофагии к детритофагии, сапрофагии и хищничеству, а у специализированных форм и к паразитизму. В способах размножения она шла от внешнего оплодотворения к внутреннему, к прямому развитию и яйцеживорождению.

В развитии рассмотренных подклассов наблюдается эволюционный параллелизм. Он морфологически выражается в тенденции к увеличению асимметрии в строении, олигомеризации радулярного аппарата, усложнении половой системы и концентрации нервной системы. В экологии и распространении параллелизм в эволюции подклассов выражается в смене местообитаний (от жизни на мелководье и на жестких фациях к обитанию на больших глубинах, на смешанных и мягких фациях, в составе эпифауны и далее инфауны, в приспособлении к существованию в пресных водах и на суше), в расширении ареала от тропических и субтропических широт в сторону умеренных и холодных областей.

Филогенетически наиболее продвинутые группы включают наибольшее число нынеживущих видов среди всех подклассов и отрядов.

Эволюционный процесс у рассмотренных брюхоногих моллюсков был неравномерным и прерывистым. Этапы наиболее интенсивного формообразования, проходившего синхронно в разных группах наблюдались в кембрийский - ордовикский, пермский - триасовый и меловой - палеогеновый периоды.

ZUSAMMENFASSUNG
.
SYSTEMATIK DER PROSOBRANCHIER-SCHNECKEN

A. N. Golikov und Y. I. Starobogatov

Die Verfasser ziehen 5 Haupt-Entwicklungslinien innerhalb der klasse der Gastropoda und unterscheiden demzufolge 5 grundsätzliche taxonomische Unterabteilungen, die in wesentlichen Zügen ihres Baues voneinander abweichen. Drei davon werden in der Regel in der Unterklasse der Prosobranchia zusammengefasst. Jedenfalls wird die Besonderheit der morphologischen Struktur und die Entwicklungsrichtung bei jeder der 3 Unterabteilungen mit denen der anderen beiden Unterklassen gleichgestellt; dies sind die Opisthobranchia und die Pulmonata. Drei unabhängige Unterklassen werden also bei den Vorderkiemer-Schnecken unterschieden: Cyclobranchia, Scutibranchia und Pectinibranchia.

Die Cyclobranchia (Kreiskiemer, d.h. was man früher Docoglossa nannte, sowie einige der paläozoischen Gruppen) stellen eine besondere Entwicklungslinie dar, erkennbar an ihrer primitiven ursprünglich symmetrischen Schale ohne Einschnitt oder Rinne, dem ursprünglichen Typus der Radula-Struktur und -Bewegung, wie sie bei anderen Schnecken nicht vorkommen und ebenso an der Struktur des Geschlechtsapparates, Magens und Nervensystems, die bei den Cyclobranchia ähnlich wie bei der Scutibranchia sind. Darüber hinaus unterstützt die Asymmetrie des Mantelkomplexes, die die Vertreter dieser Gruppe unabhängig entwickelten, die Spezialisation der Radula, die Bildung des arteriellen Bulbus und das Vorhandensein der Mantel-Nervenstränge die Meinung, dass diese Gruppe eine besondere Entwicklung durchlaufen ist. Aus diesem Grunde werden die Cyclobranchia in eine besondere Unterklasse gestellt, die die Ordnungen Helcionellida, Archinacellida (die früher zu den Monoplacophora gerechnet wurden) und Docoglossa. Der Evolutionsprozess verlief in dieser Gruppe als abnahme der Schalendimensionen und ihrer Skulptur, Verminderung der Radula-Zähne und Reduktion der besonderen Atemorgane während des Verlaufs ihrer Entwicklung.

Die übrigen Gastropoden stammen von einer alten Molluskengruppe ab, die sich aus primitiven Cyclobranchia im Kambrium entwickelt hat, diese hatten einen symmetrischen Mantelkomplex und einen Schlitz in der Mitte oder eine rinnenförmige Bildung.

Das Beibehalten der Symmetrie vom Mantelkomplex während der Weiterentwicklung, die gleichzeitige Entwicklung des Schlitzes, das gut entwickelte Epipodium und das Fehlen gewisser ganglia im Zentralnervensystem zusammen mit einer deutlichen Bildung symmetrischer Kiemenganglien erlaubt die Vereinigung der Ordnungen Dicranobranchia, Fissobranchia und Macluritida in eine besondere Unterklasse Scutibranchia (Schildkiemer). Die Weiterentwicklung innerhalb der Scutibranchier zeigt die Tendenz zur Grössenabnahme und Verminderung der Windungen, zur Trennung und Verlagerunge des Schlitzes vom Mundsaum weg, zu Zurücktreten der Spiralskulptur gegen die Längsskulptur, zur Vergrösserung der rechten Niere wegen der neuerrungenen Doppelfunktion: Exkretion and Fortpflanzung.

Die Unterklasse Pectinibranchia (Kammkiemer), die die Monotocardia (Mesogastropoda und Neogastropoda) sowie Trochacea und Neritacea von den Diotocardia (= Archeogastropoda) der früheren Klassifikationen umfasst, ist phylogenetisch am jüngsten und morphologisch am mannigfaltigsten. Sie kommt von den Scutibranchia (höchstwahrscheinlich von den Macluritida oder hat mit diesen gemeinsame Vorfahren).

Innerhalb der Pectinibranchia können 18 Ordnungen unterschieden werden, die nach einem Plan gebaut sind, und die gleiche Entwicklungsrichtung wie die ganze Unterklasse haben, aber doch auch Besonderheiten in der Evolution, in der Schalenstruktur, Fuss, Verdauungstrakt, Kieme, Zentralnervensystem, Geschlechtsapparat und Ökologie. Von diesen 18 Ordnungen werden zwei Gruppen gebildet, eine jetzt als Überordnung Pyramidellimorpha zusammengefasst, die andere umfasst die Überordnung Turbinimorpha zusammen mit stammverwandten Ordnungen die hier in die neuen Überordnungen Neritimorpha, Paludinimorpha, Littorinimorpha und Cerithiimorpha gestellt werden.

Die Gesamtentwicklung der Pectinibranchia, die sich ähnlich in verschiedenen Überordnungen und Ordnungen wiederholt, ist bezeichnet durch Nachlassen insbesondere der Spiralskulptur, Bildung eines Siphos statt des Epipodiums, Kieferreduktion, Verkleinerung der Radula die in verschiedenen Gruppen verschieden vor sich geht, Zunahme der Asymmetrie des Mantelkomplexes, Bildung einer Kammkieme und eines Osphradiums, Umbildung der rechten Niere zum Gonodukt, Konzentration und Integration des Zentralnervenystems. Die Entwicklung innerhalb der verschiedenen Untergruppen der Pectinibranchier verlaufen parallel von Mikrophagie, Sestonophagie und Phytophagie zur Detritophagie, Saprophagie, zum Beutefang und bei stark spezialisierten Formen zum Parasitismus. In der Fortpflanzung folgt auf äussere Befruchtung die innere, Aufgabe des Larvenstadiums und Ovoviviparie.

Parallelismus in der Entwicklung der betrachteten Unterklassen ist vorhanden. Er zeigt sich morphologisch in zunehmender Asymmetrie des Baues, Verkleinerung des Radulaapparates, Komplizierung der Fortpflanzungsorgane und stärkerer Konzentration des Nervensystems. In bezug auf Ökologie und Verbreitung zeigt sich die Parallelentwicklung innerhalb der Unterklassen im Wechsel des Lebensraumes (vom Leben im flachen Wasser und auf hartem Boden zum Leben in grösseren Tiefen auf gemischten und weichen Substraten, zwischen Epifauna und später Infauna), im Übergang ins Süsswasser und aufs trockene Land, in der Verbreitung von tropischen und subtropischen Breiten nach gemässigten und kalten Gebieten.

Die phylogenetisch höchstentwickelten Gruppen haben die grösste Zahl lebender Arten innerhalb allen Unterklassen und Ordnungen.

Der Entwicklungsprozess bei den betrachteten Schnecken war ungleichmässig und mit Unterbrechungen. Die Zeiten intensivster Artenbildung waren zugleich bei den verschidenen Gruppen vom Kambrium bis Ordovicium, vom Perm zur Trias und von der Kreide zum Paläogen.

H.Z.

RÉSUMÉ

SYSTÉMATIQUE DES GASTROPODES PROSOBRANCHES

A. N. Golikov et Y. I. Starobogatov

Les auteurs tracent 5 principales lignes évolutives dans la classe des Gastropoda, et à partir de là distinguent 5 principales subdivisions taxonomiques, qui diffèrent par les caractères essentiels de leur structure. Trois de ceux-ci sont, selon la règle, réunis dans la sous-classe des Prosobranchia. Cependant l'originalité de la structure morphologique et l'orientation évolutive dans chacune de ces subdivisions apparaissent comme équivalentes à celles des 2 autres sous-classes de Gastropodes, c'est-à-dire les Opisthobranchia et les Pulmonata. Trois sous-classes indépendantes sont en conséquence reconnues chez les prosobranches gastropodes: Cyclobranchia, Scutibranchia et Pectinibranchia.

Les Cyclobranchia (c'est-à-dire les anciens Docoglossa et quelques espèces des groupes Paléozoïques) présentent une ligne d'évolution particulière, mise en évidence par leur coquille primaire, primitivement symétrique, dépourvue de toute incision ou sulcus, par le type archaïque de la radula tant dans sa structure que son mouvement, caractères non partagés par tous les autres gastropodes, comme d'ailleurs la structure du système reproducteur, de l'estomac et du système nerveux, qui, chez les Cyclobranchia sont semblables à ceux des Scutibranches.

De plus, l'asymétrie du complexe palléal, qui se développe indépendamment chez les représentants de ce groupe, la spécialisation de la radula, le développement du bulbe artériel et la présence de cordons nerveux palléaux, font penser que ce groupe a un type d'évolution distinct. A partir de ces considérations, les Cyclobranchia ont été placés à part dans une sous-classe spéciale, qui embrasse les ordres Helcionellida, Archinacellida (précédemment classés parmi les Monoplacophora) et Docoglossa. Le processus d'évolution s'est morphologiquement exprimé à l'intérieur de ce groupe par la diminution des dimensions et de l'ornementation de la coquille, par une oligomérisation de la radula et par une réduction des organes spécialisés dans la respiration au cours de leur développement.

Le reste des gastropodes prend son origine à partir d'anciens groupes de mollusques, évoluant à partir de Cyclobranchia primitifs du Cambrien; ces mollusques ont un complex palléal symétrique et une fissure disposée médialement (sélénizone) ou projection sulciforme.

Le maintien de la symétrie du complexe du manteau au cours de l'évolution, le développement parallèle de la fissure, l'épipodium bien développé, l'absence de ganglions bien marqués dans le système nerveux central avec en même temps une symétrie bien nette des ganglions branchiaux, tous ces caractères ont permis l'unification des ordres Dicranobranchia, Fissobranchia et Macluritida en une sous-classe distincte, celle des Scutibranchia. L'évolution à l'intérieur des Scutibranchia montre une tendance à une réduction de la taille, à un moindre degré d'enroulement de la coquille, à une séparation et à un déplacement de la sélénizone par rapport au péristome, à la diminution de la sculpture spirale par rapport à la sculpture axiale, à l'augmentation de taille du rein droit due à la récente stabilisation de sa double fonction, celle d'excrétion et de reproduction.

La sous-classe des Pectinibranchia, comprenant les Monotocardia (Mesogastropoda et Neogastropoda) ainsi que les Trochacea et Neritacea parmi les Diotocardia (= Archeogastropoda) des précédentes classifications, est phylogénétiquement le plus récent et le plus diversifié morphologiquement; ses origines à l'intérieur des Scutibranchia (plus vraisemblablement des Macluritida ou de leurs ancêtres communs).

Chez les Pectinibranchia on peut distinguer 18 ordres qui partagent un plan commun de structure et suivent la tendance évolutive générale de l'ensemble de la sous-classe, mais qui ont déjà une ligne évolutive spéciale et une particulière structure de la coquille, du pied, de l'appareil digestif, des branchies, du système nerveux central et de l'appareil reproducteur, ainsi qu'une écologie différente. De ces 18 ordres, les premiers les 2 groupes suivants. L'un, maintenant unifié dans le superordre des Pyramidellimorpha et l'autre comprenant le superordre des Turbinimorpha et d'autres ordres voisins phylogénétiquement rassemblés dans les nouveaux superordres Neritimorpha, Paludinimorpha, Littorinimorpha et Cerithiimorpha.

Le développement évolutif des Pectinibranchia, qui se manifeste souvent de la même façon dans les différents ordres et sous-ordres, s'exprime morphologiquement par: diminution de la sculpture, surtout spirale; formation d'un processus siphonal en l'absence d'un épipodium; réduction de la mâchoire, oligomérisation de la radula, accomplies différemment dans les différents groupes; augmentation de l'asymétrie du complexe palléal; formation d'une cténidie pectinée et d'une osphradie; transformation du rein droit en gonoducte rénal; concentration et intégration du système nerveux central. L'évolution à l'intérieur des différentes subdivisions des Pectinibranchia suit une voie parallèle, depuis les ancestrales microphagie, sestonophagie et phytophagie, jusqu'aux détritophagie, saprophagie et prédation et, pour des formes spécialisées, jusqu'au parasitisme. Quant au mode de reproduction, il passe de la fécondation externe à l'interne, au développement direct et à l'ovoviviparité.

On peut percevoir un certain parallélisme évolutif dans le développement des sous-classes considérées. Il est exprimé par la tendance à l'augmentation de l'asymétrie de structure, l'oligomérisation de l'appareil radulaire, une plus grande complexité de l'appareil reproducteur et une concentration plus prononcée du système nerveux. En écologie et dans la répartition géographique, le parallélisme d'évolution entre les sous-classes se manifeste par un changement d'habitat (de la vie en eau peu profonde et sur substrat dur à celle à plus grandes profondeurs, sur fonds mixtes ou meubles, en tant qu'épifaune et plus tard d'endofaune), par l'expansion de la distribution des latitudes tropicales et subtropicales vers les régions tempérées et froides.

Les groupes les plus avancés phylogénétiquement ont le plus grand nombre d'espèces vivantes à l'intérieur de toutes les sous-classes et d'ordres.

Le processus évolutif à l'intérieur des Gastropodes considérés a été inégal et intermittent. Les stades les plus intenses dans le processus ont eu lieu simultanément dans différents groupes pendant les périodes Cambrien-Ordovicien, Permien-Triasique et Crétacé-Paléogène.

A.L.

SISTEMATICA DE GASTROPODOS PROSOBRANQUIOS

A. N. Golikov y Y. I. Starobogatov

Los autores trazan 5 ramas de evolución principales dentre de la clase Gastropoda, distinguiendo así 5 subdivisiones taxonómicas mayores que difieren en los caracteres estructurales principales. Tres de estas se unen, corrientemente, en la subclase Prosobranchia; sin embargo, la originalidad de sus caracteristicas, y el sentido de la evolución en cada una de estas tres subdivisiones, tienen valor equivalente a los de las otras 2 subclases, Opisthobranchia y Pulmonata. Por consiguiente se reconocen aqui como tres subclases independientes: Cyclobranchia, Scutibranchia y Pectinibranchia.

Los Cyclobranchia (los llamados Docoglossa, y algunos de los grupos paleozoicos) presentan una evolución particular, demonstrable por su concha primitiva, simétrica y sin surco, por su arcaica estructura y movimiento de la rádula, tipo que no se encuentra en otros gastropodos, asi como también por la estructura de los sistemas reproductor y nervioso, y del estómago, que son similares a la de Scutibranchia. Además, la asimetría del complejo paleal que se desarrolló independientemente, la especialización radular, presencia de cordones nerviosos en el manto, y desarrollo del bulbo arterial, soportan la opinión de que este grupo tuvo un tipo de evolución distinto. Estas consideraciones separan los Cyclobranchia en una subclase especial, que embraza los ordenes Helcionellida, Archinacellida (que antes se incluían en los Monoplacophora) y Docoglossa. El proceso evolutivo se demuestra morfológicamente por la redución en tamaño y escultura de la concha, la oligomerización de la rádula, y reductión de los órganos respiratorios especialidos.

El resto de los gastropodos tuvieron su origen en un antiguo grupo de los Cyclobranchia primitivos del Cámbrico; esos moluscos tenian un manto simétrico complejo, fisura media (selenizona) o proyección sulciforme.

El mantenimiento de la simetria de la complejo del manto durante la evolución, el desarrollo fisural paralelo, epipodio bien desarrollado, y la ausencia de ganglios marcados en el sistema nervioso central mientras qui tienen ganglios branquiales simétricos muy notables, permiten la unificación de los ordenes Dicranobranchia, Fissobranchia y Macluritida, en una clase separada, Scutibranchia. La evolución de los Scutibranchia muestra una tendencia hacia la reducción de tamaño y grado en el arrollamiento de la concha, hacia la separación y desplazamiento de la selenizona de el peristoma, la diminución de la escultura espiral comparada con la axial, y el aumento en tamaño del riñón derecho debido a su doble función—de establización reciente—de excreción y reproducción.

La subclase Pectinibranchia, incluyendo Monotocardia (Mesogastropoda y Neogastropoda) así como Trochacea y Neritacea de los Diotocardia (= Archeogastropoda) de las clasifiaiones corrientes, es la más jóven filogenéticamente y la más diversificada. Se originó dentro de los Scutibranchia (más probablemente de los Macluritida o sus antecesores comunes).

Dentro de los Pectinibranchia pueden distinguirse 18 ordenes con un plan de estructura común que sigue la linea evolutiva geral de la entera subclase, cada una con particularidades especiales y diversas estructuras de la concha, pié, sistema digestivo, branquias, sistema nervioso y reproductivo, así como ecología. De estos 18 ordenes, los primeros en divergencia fueron 2 grupos, uno ahora unido en el supeorden Pyramidellimorpha y el otro comprendiendo el superorden Turbinimorpha, junto con ordenes filogeneticamente relacionados combinados aquí en los nuevos superordenes Neritimorpha, Paludinimorpha, Littorinimorpha y Cerithiimorpha.

La evolución de los Pectinibranchia—que se manifiesta similarmente en diferentes ordenes y superordenes—se demuestra en la morfología de: la reducción (particularmente espiral) de la escultura; formación de un proceso sifonal en ausencia del epipodio; reducción de la mandíbula; oligomerización de la rádula que se produjo en forma distinta en los diferentes grupos; aumento de la asimetría del complejo paleal; formación de un ctenidium pectinado y osfradio; transformación del riñón derecho en un gonoducto renal; concentración e integración del sistema nervioso central. Esta evolución en los diferentes grupos de Pectinibranchia tomó caminos paralelos, desde una microfagia y sestonofagia ancestral y phytofagia, hacia detritofagia, saprofagia y predación, y, dentro de formas especializadas, hacia parasitismo. En el modo de reprodución pasaron de fertilizacion externa a interna, al desarrollo directo y ovoviparidad.

Un paralelismo evolutivo se percibe en las subclases consideradas. Esto se muestra morfológicamente en la tendencia hacia un aumento en la asimetría de la estructura, oligomerización del aparato radular, mayor complejidad del sistema reproductor, y una concentración más pronunciada del sistema nervioso. En ecología y distribución, tal paralelismo se manifiesta en los cambios de habitat (desde las aguas poco profundas sobre fondos duros, a la vida en las grandes profundidades de fondos blandos y mixtos, dentro de la epifauna y más tarde infauna), en la adaptación a las aguas dulces y vida terrestre, y en la expansión desde latitudes tropical y subtropicales hacia regiones templadas y frías.

   Los grupos más avanzados filogenéticamente tienen el más grande numero de especies vivientes dentro de todas las subclases y en los ordenes.
   La evolución de los gastropodos considerados fué despareja e intermitente. Los estados más intensos en el proceso formativo aparecieron simultaneamente dentro de los diferentes grupos en el Cámbrico-Ordoviciano, Permo-Triásico y el Cretáceo-Paleogeno.

                                                                                J. J. P.